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ADVERTISEMENT.

The Committee appointed by the *Royal Society* to direct the publication of the *Philosophical Transactions* take this opportunity to acquaint the public that it fully appears, as well from the Council-books and Journals of the Society as from repeated declarations which have been made in several former *Transactions*, that the printing of them was always, from time to time, the single act of the respective Secretaries till the Forty seventh Volume; the Society, as a Body, never interesting themselves any further in their publication than by occasionally recommending the revival of them to some of their Secretaries, when, from the particular circumstances of their affairs, the *Transactions* had happened for any length of time to be intermitted. And this seems principally to have been done with a view to satisfy the public that their usual meetings were then continued, for the improvement of knowledge and benefit of mankind: the great ends of their first institution by the Royal Charters, and which they have ever since steadily pursued.

But the Society being of late years greatly enlarged, and their communications more numerous, it was thought advisable that a Committee of their members should be appointed to reconsider the papers read before them, and select out of them such as they should judge most proper for publication in the future *Transactions;* which was accordingly done upon the 26th of March, 1752. And the grounds of their choice are, and will continue to be, the importance and singularity of the subjects, or the advantageous manner of treating them; without pretending to answer for the certainty of the facts, or propriety of the reasonings contained in the several papers so published, which must still rest on the credit or judgment of their respective authors.

It is likewise necessary on this occasion to remark, that it is an established rule of the Society, to which they will always adhere, never to give their opinion, as a Body, upon any subject, either of Nature or Art, that comes before them. And therefore the thanks, which are frequently proposed from the Chair, to be given to the authors of such papers as are read at their accustomed meetings, or to the persons through whose hands they received them, are to be considered in no other light than as a matter of civility, in return for the respect shown to the Society by those communications. The like also is to be said with regard to the several projects, inventions, and curiosities of various kinds, which are often exhibited to the Society; the authors whereof, or those who exhibit them, frequently take the liberty to report, and even to certify in the public newspapers, that they have met with the highest applause and approbation. And therefore it is hoped that no regard will hereafter be paid to such reports and public notices; which in some instances have been too lightly credited, to the dishonour of the Society.

LIST OF INSTITUTIONS ENTITLED TO RECEIVE THE PHILOSOPHICAL TRANSACTIONS OR PROCEEDINGS OF THE ROYAL SOCIETY.

Institutions marked A are entitled to receive Philosophical Transactions, Series A, and Proceedings
" " B " " " " Series B, and Proceedings.
" " AB " " " " Series A and B, and Proceedings.
" " *p* " " Proceedings only.

America (Central).
- Mexico.
  - *p.* Sociedad Cientifica "Antonio Alzate."

America (North). (See UNITED STATES.)

America (South).
- Buenos Ayres.
  - AB. Museo Publico.
- Caracas.
  - B. University Library.
- Cordova.
  - AB. Academia Nacional de Ciencias.
- Rio de Janeiro.
  - *p.* Imperial Observatorio.

Australia.
- Adelaide.
  - *p.* Royal Society of South Australia.
- Brisbane.
  - *p.* Royal Society of Queensland.
- Melbourne.
  - *p.* Observatory.
  - *p.* Royal Society of Victoria.
  - AB. University Library.
- Sydney.
  - *p.* Linnean Society of New South Wales.
  - AB. Royal Society of New South Wales.
  - AB. University Library

Austria.
- Agram.
  - *p.* Societas Historico-Naturalis Croatica.
- Brünn.
  - AB. Naturforschender Verein.
- Gratz.
  - AB. Naturwissenschaftlicher Verein für Steiermark.
- Hermannstadt.
  - Siebenbürgischer Verein für die Naturwissenschaften.

Austria (continued).
- Innsbruck.
  - AB. Das Ferdinandeum
  - *p.* Naturwissenschaftlich - Medicinischer Verein.
- Klausenburg.
  - AB. Az Erdélyi Muzeum. Das siebenbürgische Museum.
- Prague.
  - AB. Königliche Böhmische Gesellschaft der Wissenschaften
- Schemnitz.
  - *p* K. Ungarische Berg- und Forst-Akademie.
- Trieste.
  - B. Museo di Storia Naturali.
  - *p.* Società Adriatica di Scienze Naturali.
- Vienna.
  - *p.* Anthropologische Gesellschaft.
  - AB. Kaiserliche Akademie der Wissenschaften.
  - *p.* K.K. Geographische Gesellschaft.
  - AB. K.K. Geologische Reichsanstalt.
  - B. K.K. Zoologisch-Botanische Gesellschaft.
  - B. Naturhistorisches Hof Museum.
  - *p.* Œsterreichische Gesellschaft fur Meteorologie.

Belgium.
- Brussels.
  - B. Académie Royale de Médecine
  - AB. Académie Royale des Sciences.
  - B. Musée Royal d'Histoire Naturelle de Belgique.
  - *p.* Observatoire Royale
  - *p.* Société Malacologique de Belgique.
- Ghent.
  - AB. University.
- Liége.
  - AB. Société des Sciences.

Belgium (continued).
- Liége (continued)
  - *p* Société Géologique de Belgique.
- Louvain.
  - AB. L'Université.

Canada.
- Hamilton
  - *p.* Scientific Association.
- Montreal.
  - AB. McGill College.
  - *p.* Natural History Society.
- Ottawa
  - AB Geological Survey of Canada.
- Toronto.
  - *p.* Canadian Institute.
  - AB University.

Cape of Good Hope.
  - A. Observatory.
  - AB. South African Library.

Ceylon.
- Colombo
  - B. Museum.

China.
- Shanghai.
  - *p.* China Branch of the Royal Asiatic Society.

Denmark.
- Copenhagen.
  - AB. Kongelige Danske Videnskabernes Selskab.

England and Wales.
- Birmingham.
  - AB. Free Central Library.
  - AB. Mason College.
- Bristol.
  - *p.* Merchant Venturers' School.
- Cambridge.
  - AB. Philosophical Society.
  - *p.* Union Society.
- Cooper's Hill.
  - AB. Engineering College.
- Dudley.
  - *p.* Dudley and Midland Geological and Scientific Society.
- Essex.
  - *p.* Essex Field Club.
- Greenwich.
  - A. Observatory.
- Kew.
  - AB. Royal Gardens.
- Leeds.
  - [illegible] Philosophical Society.
  - [illegible] Yorkshire College.

England and Wales (continued)
- Liverpool (continued)
  - *p.* Literary and Philosophical Society.
  - A. Observatory.
  - AB. University College.
- London.
  - AB. Admiralty.
  - *p.* Anthropological Institute
  - B. British Museum (Nat. Hist.)
  - A Chemical Society
  - *p.* "Electrician," Editor of the.
  - B. Entomological Society.
  - AB. Geological Society.
  - AB. Geological Survey of Great Britain
  - *p.* Geologists' Association.
  - AB. Guildhall Library.
  - A. Institution of Civil Engineers
  - A. Institution of Mechanical Engineers.
  - A. Institution of Naval Architects.
  - *p.* Iron and Steel Institute
  - B. Linnean Society.
  - AB. London Institution.
  - *p.* London Library.
  - A. Mathematical Society.
  - *p.* Meteorological Office
  - *p.* Odontological Society.
  - *p.* Pharmaceutical Society.
  - *p.* Physical Society.
  - *p.* Quekett Microscopical Club
  - *p.* Royal Asiatic Society.
  - A. Royal Astronomical Society.
  - B. Royal College of Physicians.
  - B. Royal College of Surgeons.
  - *p.* Royal Engineers (for Libraries abroad, six copies).
  - AB. Royal Engineers. Head Quarters Library.
  - *p.* Royal Geographical Society.
  - *p.* Royal Horticultural Society
  - *p.* Royal Institute of British Architects.
  - AB. Royal Institution of Great Britain
  - B. Royal Medical and Chirurgical Society.
  - *p.* Royal Meteorological Society.
  - *p.* Royal Microscopical Society.
  - *p.* Royal Statistical Society.
  - AB. Royal United Service Institution.
  - AB. Society of Arts.
  - *p.* Society of Biblical Archæology.
  - *p.* Standard Weights and Measures Department.
  - AB. The Queen's Library.
  - AB. The War Office.
  - AB. University College.
  - *p.* Victoria Institute.
  - B. Zoological Society.

England and Wales (continued)

- Manchester.
  - AB. Free Library.
  - AB. Literary and Philosophical Society
  - *p.* Geological Society.
  - AB. Owens College.
- Netley.
  - *p.* Royal Victoria Hospital.
- Newcastle
  - AB. Free Library
  - *p.* North of England Institute of Mining and Mechanical Engineers
  - *p.* Society of Chemical Industry (Newcastle Section)
- Norwich.
  - *p.* Norfolk and Norwich Literary Institution
- Oxford.
  - *p.* Ashmolean Society.
  - AB. Radcliffe Library.
  - A. Radcliffe Observatory.
- Penzance.
  - *p.* Geological Society of Cornwall
- Plymouth.
  - B. Marine Biological Association.
  - *p.* Plymouth Institution.
- Richmond.
  - A. "Kew" Observatory.
- Salford.
  - *p.* Royal Museum and Library.
- Stonyhurst
  - *p.* The College
- Swansea.
  - AB. Royal Institution.
- Woolwich.
  - AB Royal Artillery Library.

Finland.

- Helsingfors.
  - AB Société des Sciences.
  - *p.* Societas pro Fauna et Flora Fennica.

France.

- Bordeaux.
  - *p.* Académie des Sciences.
  - *p.* Faculté des Sciences.
  - *p.* Société de Médecine et de Chirurgie.
  - *p.* Société des Sciences Physiques et Naturelles.
- Cherbourg.
  - *p.* Société des Sciences Naturelles.
- Dijon.
  - *p.* Académie des Sciences.
- Lille.
  - *p.* Faculté des Sciences.

France (continued)

- Lyons.
  - AB Académie des Sciences, Belles-Lettres et Arts.
- Marseilles
  - *p* Faculté des Sciences
- Montpellier.
  - AB Académie des Sciences et Lettres
  - B Faculté de Médecine
- Paris
  - AB Académie des Sciences de l'Institut.
  - *p* Association Française pour l'Avancement des Sciences.
  - *p.* Conservatoire des Arts et Métiers
  - *p* Cosmos (M. L'ABBÉ VALETTE)
  - AB Dépôt de la Marine
  - AB. École des Mines
  - AB. École Normale Supérieure
  - AB. École Polytechnique
  - AB. Faculté des Sciences de la Sorbonne.
  - AB. Jardin des Plantes
  - A L'Observatoire
  - *p.* Revue Internationale de l'Électricité
  - *p.* Revue Scientifique (Mons. RICHET).
  - *p.* Société de Biologie
  - AB. Société d'Encouragement pour l'Industrie Nationale.
  - *p* Société de Physique.
  - AB Société de Géographie.
  - B Société Entomologique
  - AB. Société Géologique.
  - *p* Société Mathématique
  - *p* Société Météorologique de France.
- Toulouse.
  - AB. Académie des Sciences
  - A. Faculté des Sciences

Germany.

- Berlin.
  - A. Deutsche Chemische Gesellschaft.
  - A. Die Sternwarte.
  - AB. Königliche Akademie der Wissenschaften.
  - A Physikalische Gesellschaft.
- Bonn.
  - AB. Universitat.
- Bremen.
  - *p.* Naturwissenschaftlicher Verein
- Breslau.
  - *p.* Schlesische Gesellschaft fur Vaterländische Kultur.
- Brunswick.
  - *p.* Verein für Naturwissenschaft.
- Carlsruhe. See Karlsruhe.
- Danzig.
  - AB. Naturforschende Gesellschaft.

Germany (continued)

Dresden.
- *p.* Verein für Erdkunde

Emden.
- *p.* Naturforschende Gesellschaft

Erlangen.
- AB Physikalisch-Medicinische Societät.

Frankfurt-am-Main.
- AB. Senckenbergische Naturforschende Gesellschaft.
- *p* Zoologische Gesellschaft.

Frankfurt-am-Oder.
- *p* Naturwissenschaftlicher Verein.

Freiburg-im-Breisgau.
- AB. Universität.

Giessen.
- AB. Grossherzogliche Universität.

Görlitz.
- *p.* Naturforschende Gesellschaft

Göttingen.
- AB. Königliche Gesellschaft der Wissenschaften.

Halle.
- AB. Kaiserliche Leopoldino - Carolinische Deutsche Akademie der Naturforscher.
- *p.* Naturwissenschaftlicher Verein für Sachsen und Thüringen.

Hamburg.
- AB. Naturwissenschaftlicher Verein.

Heidelberg
- *p.* Naturhistorisch-Medizinische Gesellschaft.
- AB Universität.

Jena.
- *p.* Medicinisch-Naturwissenschaftliche Gesellschaft.

Karlsruhe.
- A. Grossherzogliche Sternwarte.

Kiel.
- A. Sternwarte.
- AB. Universität.

Königsberg.
- [illegible] Königliche Physikalisch - Ökonomische Gesellschaft.

Leipzig.
- [illegible] Annalen der Physik und Chemie.
- [illegible]
- [illegible] Gesellschaft der

Germany (continued)

Munich
- AB. Königliche Bayerische Akademie der Wissenschaften.
- *p.* Zeitschrift für Biologie.

Münster.
- AB. Königliche Theologische und Philosophische Akademie.

Rostock.
- AB. Universität.

Strassburg.
- AB. Universitat.

Tübingen.
- AB. Universität.

Würzburg.
- AB. Physikalisch-Medicinische Gesellschaft

Holland. (See NETHERLANDS)

Hungary.

Pesth.
- *p.* Königl. Ungarische Geologische Anstalt.
- AB. Á Magyar Tudós Társaság. Die Ungarische Akademie der Wissenschaften.

India.

Bombay.
- AB. Elphinstone College.

Calcutta.
- AB. Asiatic Society of Bengal.
- AB. Indian Museum.
- *p.* Great Trigonometrical Survey of India
- *p.* The Meteorological Reporter to the Government of India.

Madras.
- B. Central Museum.
- A. Observatory.

Roorkee
- *p.* Roorkee College.

Ireland.

Armagh.
- A. Observatory.

Belfast.
- AB. Queen's College.

Cork.
- *p.* Philosophical Society.
- AB. Queen's College.

Dublin.
- A. Observatory.
- AB. National Library of Ireland.
- B. Royal College of Surgeons in Ireland.
- AB. Royal Dublin Society.
- AB. Royal Irish Academy.

Galway.
- [illegible] Queen's College.

Italy.

- Bologna.
  - AB. Accademia delle Scienze dell' Istituto.
- Catania
  - AB Accademia Gioenia di Scienze Naturali.
- Florence.
  - *p* Biblioteca Nazionale Centrale.
  - AB. Reale Museo di Fisica.
- Milan.
  - AB. Reale Istituto Lombardo di Scienze, Lettere ed Arti
  - AB Società Italiana di Scienze Naturali.
- Naples.
  - AB. Società Reale, Accademia delle Scienze
  - B. Stazione Zoologica (Dr. DOHRN).
- Padua.
  - *p* University
- Palermo.
  - A Circolo Matematico.
  - AB Consiglio di Perfezionamento (Società di Scienze Naturali ed Economiche).
  - A. Reale Osservatorio.
- Pisa.
  - *p.* Società Toscana di Scienze Naturali.
- Rome.
  - *p.* Accademia Pontificia de' Nuovi Lincei
  - A. Osservatorio del Collegio Romano
  - AB. Reale Accademia dei Lincei.
  - *p* R Comitato Geologico d' Italia.
  - AB Società Italiana delle Scienze
- Turin.
  - *p.* Laboratorio di Fisiologia.
  - AB. Reale Accademia delle Scienze.
- Venice.
  - *p.* Ateneo Veneto.
  - AB. Reale Istituto Veneto di Scienze, Lettere ed Arti.

Japan.

- Tokiô.
  - AB. Imperial University
- Yokohama.
  - *p.* Asiatic Society of Japan.

Java.

- Batavia.
  - AB. Bataviaasch Genootschap van Kunsten en Wetenschappen.
- Buitenzorg.
  - *p.* Jardin Botanique

Malta.

- *p.* Public Library.

Mauritius.

- *p.* Royal Society of Arts and Sciences

Netherlands.

- Amsterdam.
  - AB. Koninklijke Akademie van Wetenschappen.
  - *p.* Zoologisch Genootschap 'Natura Artis Magistra'
- Delft
  - *p.* École Polytechnique.
- Haarlem.
  - AB. Hollandsche Maatschappij der Wetenschappen
  - *p.* Musée Teyler.
- Leyden
  - AB University
- Luxembourg.
  - *p* Société des Sciences Naturelles
- Rotterdam.
  - AB. Bataafsch Genootschap der Proefondervindelijke Wijsbegeerte.
- Utrecht.
  - AB. Provinciaal Genootschap van Kunsten en Wetenschappen.

New Zealand

- Wellington.
  - AB. New Zealand Institute

Norway.

- Bergen
  - AB. Bergenske Museum
- Christiania.
  - AB Kongelige Norske Frederiks Universitet.
- Tromsoe.
  - *p.* Museum.
- Trondhjem.
  - AB. Kongelige Norske Videnskabers Selskab

Nova Scotia.

- Windsor.
  - *p.* King's College Library

Portugal.

- Coimbra.
  - AB Universidade.
- Lisbon.
  - AB. Academia Real das Sciencias.
  - *p.* Secção dos Trabalhos Geologicos de Portugal.

Russia.

- Kazan.
  - AB. Imperatorsky Kazansky Universitet.
- Kharkoff.
  - *p.* Section Médicale de la Société des Sciences Expérimentales, Université de Kharkow.
- Kieff.
  - *p.* Société des Naturalistes.
- Moscow.
  - AB. Le Musée Publique.
  - B. Société Impériale des Naturalistes.

Russia (continued).

- Odessa.
  - *p.* Société des Naturalistes de la Nouvelle-Russie
- Pulkowa.
  - A. Nikolai Haupt-Sternwarte
- St. Petersburg
  - AB. Académie Impériale des Sciences
  - AB. Comité Géologique.
  - *p.* Compass Observatory.
  - A. L'Observatoire Physique Central

Scotland.

- Aberdeen.
  - AB. University.
- Edinburgh.
  - *p.* Geological Society.
  - A Observatory.
  - *p.* Royal Medical Society
  - *p.* Royal Physical Society.
  - *p.* Royal Scottish Society of Arts
  - AB Royal Society.
- Glasgow.
  - AB. Mitchell Free Library.
  - *p.* Philosophical Society

Servia.

- Belgrade.
  - *p.* Académie Royale de Serbie.

Spain.

- Cadiz.
  - A. Observatorio de San Fernando.
- Madrid.
  - *p.* Comision del Mapa Geologico de España.
  - AB. Real Academia de Ciencias

Sweden.

- Gottenburg.
  - AB. Kongl. Vetenskaps och Vitterhets Samhälle.
- Lund.
  - AB. Universitet.
- Stockholm.
  - A. Acta Mathematica.
  - AB. Kongliga Svenska Vetenskaps-Akademie.
  - AB. Sveriges Geologiska Undersökning.
- Upsala.
  - AB. Universitet.

Switzerland.

- Basel.
  - *p.* Naturforschende Gesellschaft.
- Bern.
  - AB. Allg. Schweizerische Gesellschaft.
  - *p.* Naturforschende Gesellschaft.

Switzerland (continued)

- Geneva
  - AB. Société de Physique et d'Histoire Naturelle
  - AB Institut National Genevois
- Lausanne
  - *p.* Société Vaudoise des Sciences Naturelles
- Neuchâtel
  - *p* Société des Sciences Naturelles
  - *p* Astronomische Mittheilungen (Professor R Wolf).
- Zürich.
  - AB. Das Schweizerische Polytechnikum
  - *p* Naturforschende Gesellschaft

Tasmania.

- Hobart.
  - *p.* Royal Society of Tasmania

United States.

- Albany.
  - AB. New York State Library
- Annapolis.
  - AB. Naval Academy.
- Baltimore.
  - AB. Johns Hopkins University
- Boston.
  - AB. American Academy of Sciences
  - B. Boston Society of Natural History
  - A. Technological Institute
- Brooklyn.
  - AB. Brooklyn Library (N.Y.).
- Cambridge.
  - AB. Harvard University.
- Chapel Hill (N.C.).
  - *p.* Elisha Mitchell Scientific Society
- Charleston.
  - *p.* Elliott Society of Science and Art of South Carolina.
- Chicago.
  - AB. Academy of Sciences
- Davenport (Iowa).
  - *p.* Academy of Natural Sciences
- Madison.
  - *p.* Wisconsin Academy of Science
- Mount Hamilton (California).
  - A. Lick Observatory.
  - *p.* University of California.
- Newhaven (Conn.).
  - AB. American Journal of Science.
  - AB. Connecticut Academy of Arts and Sciences.
- New York.
  - *p.* American Geographical Society.
  - *p.* American Museum of Natural History
  - *p.* New York Academy of Sciences.
  - *p.* New York Medical Journal.
  - *p.* School of Mines, Columbia College

United States (continued).

Philadelphia
- AB Academy of Natural Sciences
- AB American Philosophical Society
- *p.* Franklin Institute
- *p.* Wagner Free Institute of Science

St Louis
- *p* Academy of Science.

Salem (Mass)
- *p.* Essex Institute.
- AB. Peabody Academy of Science

San Francisco
- AB California Academy of Sciences

United States (continued)

Washington
- *p* Department of Agriculture
- A Office of the Chief Signal Officer
- AB Patent Office
- AB Smithsonian Institution
- *p* United States Commission of Fish and Fisheries
- AB United States Coast Survey
- AB United States Geological Survey
- A. United States Naval Observatory

West Point (N Y)
- AB United States Military Academy

ADJUDICATION of the MEDALS of the ROYAL SOCIETY for the year 1888, by the PRESIDENT and COUNCIL.

The COPLEY MEDAL to Professor THOMAS HENRY HUXLEY, F.R S , for his Investigations on the Morphology and Histology of Vertebrate and Invertebrate Animals, and for his services to Biological Science in general during many past years.

The RUMFORD MEDAL to Professor PIETRO TACCHINI for important and long-continued Investigations, which have largely advanced our knowledge of the Physics of the Sun.

A ROYAL MEDAL to Baron FERDINAND VON MUELLER, K.C.M.G , F R S , for his long services in Australian Exploration, and for his Investigations of the Flora of the Australian Continent

A ROYAL MEDAL to Professor OSBORNE REYNOLDS, F.R S , for his Investigations in Mathematical and Experimental Physics, and on the Application of Scientific Theory to Engineering.

The DAVY MEDAL to WILLIAM CROOKES, F.R.S , for his Investigations on the Behaviour of Substances under the Influences of the Electric Discharge in a High Vacuum.

The Bakerian Lecture, "Suggestions on the Classification of the various Species of Heavenly Bodies," was delivered by J. NORMAN LOCKYER, F.R.S.

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PHILOSOPHICAL TRANSACTIONS.

I. *A Record of Experiments upon the Functions of the Cerebral Cortex.*

By VICTOR HORSLEY, *M.B., F.R.C.S., F.R.S., Professor Superintendent of the Brown Institution, and* EDWARD ALBERT SCHÄFER, *F R.S., Jodrell Professor of Physiology in University College, London.* (*From the Physiological Laboratory, University College.*)

Received February 5,—Read February 17, 1887.

[PLATES 1–7.]

INTRODUCTORY REMARKS.

THE experiments which are here recorded are selected from a series which we have been engaged upon during the past three years, having for their object the further elucidation of the functions of the several parts of the cerebral cortex, with especial reference to localisation of the centres for voluntary action and sensation. They were undertaken by us in the hope of clearing up some of the discrepancies in the evidence offered upon those points by previous observers, and for this purpose it was important to go over ground which had already been trodden; but we subsequently found it to be necessary to investigate portions of the cortex which, probably by reason of difficulty of access, had not, so far as we could ascertain, been touched by our predecessors in this field of physiological research, and particularly the convolutions upon the mesial aspect of the hemisphere, viz., the gyrus marginalis and the gyrus fornicatus.

Methods.

The methods we have employed have been: 1. Electrical Excitation, and 2. Ablation. For the purposes of electrical excitation we have generally used a DU BOIS-REYMOND inductorium, with a metallic reed interruptor in place of the usual WAGNER hammer, so arranged that, as with the HELMHOLTZ side-wire, the primary current is never entirely opened; this method we have already described elsewhere.* The strength of the excitation used was always such as to produce no more than a slight pricking sensation on the tongue. The removal of the various parts of the cerebral cortex has in all our experiments, except the first few, been effected by the knife, or by small cutting instruments specially constructed for the purpose. We were led to adopt the knife instead of the galvanic cautery (which had been used by Professors FERRIER and YEO) on account of the greater facility with which the lesion can be limited exactly in depth and extent without risk of subsequent disintegration of the neighbouring parts, while at the same time the bleeding is not markedly greater, and is usually readily stayed by gentle pressure. All these experiments have been performed with the strictest antiseptic precautions and under carbolic spray, and the wound, after being closely stitched, has been dressed with antiseptic gauze, and this again overlaid and rendered firmly adherent to the surrounding scalp by a layer of thick collodion so as to make it impossible for the animals to tear away the dressing; at the same time, the collodion, shrinking and becoming hard in drying, serves temporarily to support the contents of the skull, and to prevent their protrusion through the aperture made by the trephine or saw. The dressing was always removed within a week after the operation, sometimes as early as the third day, and it was almost invariably found that the edges of the wound in the skin had completely united, and that the animal could safely be left without further dressing or attention. Moreover there appears to be no tendency under these circumstances for any extension of the lesion to occur by inflammation of the surrounding parts of the brain, nor do adhesions form between the surface of the brain and the enveloping membrane, except along the edges of the wound. In all the cases here recorded the animals employed have been Monkeys, but we have not confined ourselves to one kind alone, having used indiscriminately individuals belonging to various species. They have usually been kept alive for some weeks or months after the operation, sometimes being submitted to two or more successive ablations at variable intervals of time. In those cases in which the animals have died, death has very rarely been due to the shock or severity of the operation, except in the case of lesions producing very extensive motor paralysis, but has been the result of accidental causes, and especially of a sort of dysenteric diarrhœa to which Monkeys appear peculiarly liable. In most instances the animals have been purposely killed after having been sufficiently long under observation, and, the condition of the brain having been accurately recorded, the whole of the central nervous system has been preserved for future investigation. All the operations have been performed under anæsthetics, either chloroform or ether being used, almost always supplemented by the hypodermic injection of morphia (as much as from half to one grain of the acetate having usually been given). This has the great advantage of causing the animal to remain perfectly quiet for several hours after the operation, and of permitting it, during the slow process of recovery from the effects of the morphia, to become accustomed to the collodion dressing, which would otherwise be irksome, and this would lead to attempts at removal.*

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* HORSLEY and SCHÄFER, "Experiments on the Character of the Muscular Contractions which are evoked by Excitation of the various Parts of the Motor Tract." 'Journal of Physiology,' vol. 7, p. 96.

It has, however, the disadvantage that observations cannot be at once made upon the disturbance of function produced by the lesion, on account of the condition of stupor which is caused by the morphia. This disadvantage is not so great as it may at first sight seem, for such immediate observations are of less value than later ones, especially when the lesion is an extensive one, on account of the very considerable disturbance which must be temporarily produced upon the remainder of the hemisphere, partly by the blocking of the vessels of the ablated portion, and partly by the loss of support experienced by the neighbouring portions when a large piece has been removed at one operation.

We may conveniently arrange our general results according to the regions to which they respectively relate, and they will therefore be grouped under the following heads, viz :—I. Prefrontal; II. Central or Motor; III. Occipital; IV. Temporo-sphenoidal and Limbic.

I.—Results of Experiments upon the Prefrontal Region of the Hemisphere.

Results of excitation.—Electrical excitation of the anterior end of the frontal lobes has invariably yielded negative results in our hands. But behind the anterior end of the sagittal limb of the precentral sulcus the lateral movement of the head and eyes described by Ferrier† begins to be evident.

Result of ablation.—In three cases we have completely removed at one operation the anterior third or fourth of both frontal lobes, including all that part which we had found electrically inexcitable In two of these the animals rapidly recovered without showing any sign of motor paralysis,‡ nor could any deficiency of general or special sensibility be detected. One of the two Monkeys was a very tame animal, which had acquired certain tricks before the operation; these were exhibited equally well afterwards; nor was the Monkey rendered any less tame or intelligent, so far as could be detected, as the result of the lesion. In both cases the animals were under observation for nearly four months without showing any abnormal symptoms whatever. The extent of the lesion in these two cases is shown in figs. 1 and 2; and the extent in a third experiment upon this region in fig. 3 (Plate 1). As was *à fortiori* to have been expected, unilateral ablation, which we performed in one case, proved equally devoid of positive results.

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* The morphia has also appeared to us to diminish the hæmorrhage from the cut cerebral surface. This is in any case easily stayed by the application of gentle pressure.

† Ferrier, 'Functions of the Brain,' 2nd edition, p. 242

‡ After lesions of the anterior part of the frontal lobes the animals for the first few days always assume a characteristic attitude, sitting with the head bent downwards between the arms, and they appear more lethargic than is usual after operations involving other parts of the brain. But after a few days all these symptoms pass completely away, and the normal attitude and disposition are resumed.

Conclusions and remarks.—The results of our experiments upon the anterior part of the frontal lobes have been completely negative so far as electrical excitation or the permanent result of ablation are concerned. In this we are in agreement with FERRIER and YEO,* but in contradiction of the results obtained by H. MUNK.† FERRIER and YEO, it is true, describe certain transient symptoms as having been observed by them, but we have already given our reasons for regarding such immediate and only transitory effects as not to be laid too much stress upon in the determination of the function of a part. And they expressly state that in the Monkeys which they were successful in keeping alive for any considerable time no physiological defect of any kind could be substantiated.‡ MUNK, on the other hand, has described positive symptoms as resulting from extirpation of this part of the cerebrum both in Dogs and Monkeys, viz., a paresis of the trunk muscles, causing loss of rotating power if the extirpation be unilateral; and with bilateral removal in Monkeys a peculiar cat-like bending of the trunk.§ MUNK also found that electrical excitation caused contraction of the muscles of the back and abdomen, and even the diaphragm, but admits that very strong excitations are necessary to produce any effect. He attempts to explain the necessity for such strong excitation by the greater weight which the trunk muscles have to move (in proportion to their number and size?), but it seems to us that a much simpler explanation may be given, and that the results which he describes are due to the spreading to other regions of the brain of the strong currents which he confesses to have been obliged to employ. The governance of the trunk muscles, which MUNK has ascribed to the prefrontal region, belongs rather, as we shall immediately show, to the middle of the marginal convolution and the adjoining part of the external surface of the hemisphere. The discrepancy between the results of our experiments upon the ablation of this part and those of MUNK we are unable to explain otherwise than by supposing that sufficient care was not taken by MUNK to localise the lesion by the adoption of the precautions of modern antiseptic surgery. Thus he speaks of operations upon this region in the Dog as taking two or three weeks to heal in the most favourable instances, and even then as discharging pus! And, although according to this author Monkeys appear to bear the removal of portions of the brain far more easily, so far as the after-process of healing is concerned, than Dogs, yet it must be assumed that there will be a greater or less amount of inflammatory extension of the intended lesion in all cases in which antiseptic precautions are omitted. Indeed we do not hesitate to affirm, on the strength of the evidence afforded by two or three of our cases in which the wound, although at first aseptic, subsequently became septic, that all experiments upon the brain in which these precautions are neglected are not only liable to be lacking in definiteness and precision, but may even be expected to yield illusory results.

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* FERRIER and YEO, "A Record of Experiments on the Effects of Lesion of different Regions of the Cerebral Hemispheres," 'Philosophical Transactions,' 1884. See also FERRIER, 'Functions of the Brain,' p. 396. It would seem that the whole of the prefrontal region was not removed in all the cases cited by Professors FERRIER and YEO, for in many the orbital surface is left intact. On the other hand, in some the lesion encroaches above and posteriorly on the centre for movement of the head and eyes.

† H MUNK, "Ueber die Stirnlappen des Grosshirns," 'Sitzungsberichte der k. Preussischen Akademie,' 1882.

‡ See especially their remarks upon Case No. 22 recorded by them, in which the lesion of the prefrontal region was very complete.

§ Probably the attitude we have described in the note on the previous page. MUNK also affirms that cutaneous and muscular sensibility is lost in the trunk after this lesion, and indeed in all these cases of cortical lesion refers the resulting muscular paralysis to the loss of such sensibility; this is, however, a question which will be discussed later on.

No doubt the same remark will apply to the earlier experiments of FERRIER, which were performed without the employment of such precautions, and were obviously followed in many cases by inflammatory extension of the original lesion. The argument that such extension must have taken place, which with other arguments MUNK urges with somewhat unnecessary bitterness ('Functionen der Grosshirnrinde —Erste Mittheilung'), attempting to discredit the whole of FERRIER'S work in this direction, can be used with equal force against many of the results obtained by himself.

II.—RESULTS OF EXPERIMENTS UPON THE MOTOR REGION OF THE CEREBRAL CORTEX.

Results of excitation of the external surface.—Excitation of the external surface of the hemisphere has in our hands yielded results which are generally similar to those described by FERRIER,[*] which they may be said to extend and confirm, with some exception as to detail. It will be remembered that besides certain areas close to the great longitudinal fissures, which are concerned with movements of the hind-limb, the principal movements obtained by FERRIER by stimulation of the excitable portion of the external surface were: (1) On the middle of the frontal lobe—movements of the head and eyes. (2) Just behind this area on the ascending frontal—movements of the hand and arm. (3) On the ascending parietal—movements of the fingers and wrist. And (4) around the lower end of the fissure of ROLANDO, including parts of both central convolutions—movements of the face, jaw, and tongue (several of these movements being still further differentiated). Our experiments show that the motor portion of the cerebral cortex may be mapped out into a certain number of main areas, each of which is chiefly concerned with the movements of a particular part or limb, and in some of which certain centres concerned with more specialised movements may be marked out.* It will be convenient, in the first place, to describe those portions of these areas which are seen upon the external surface of the brain (see Diagram I), and subsequently those which are met with upon the mesial surface.†

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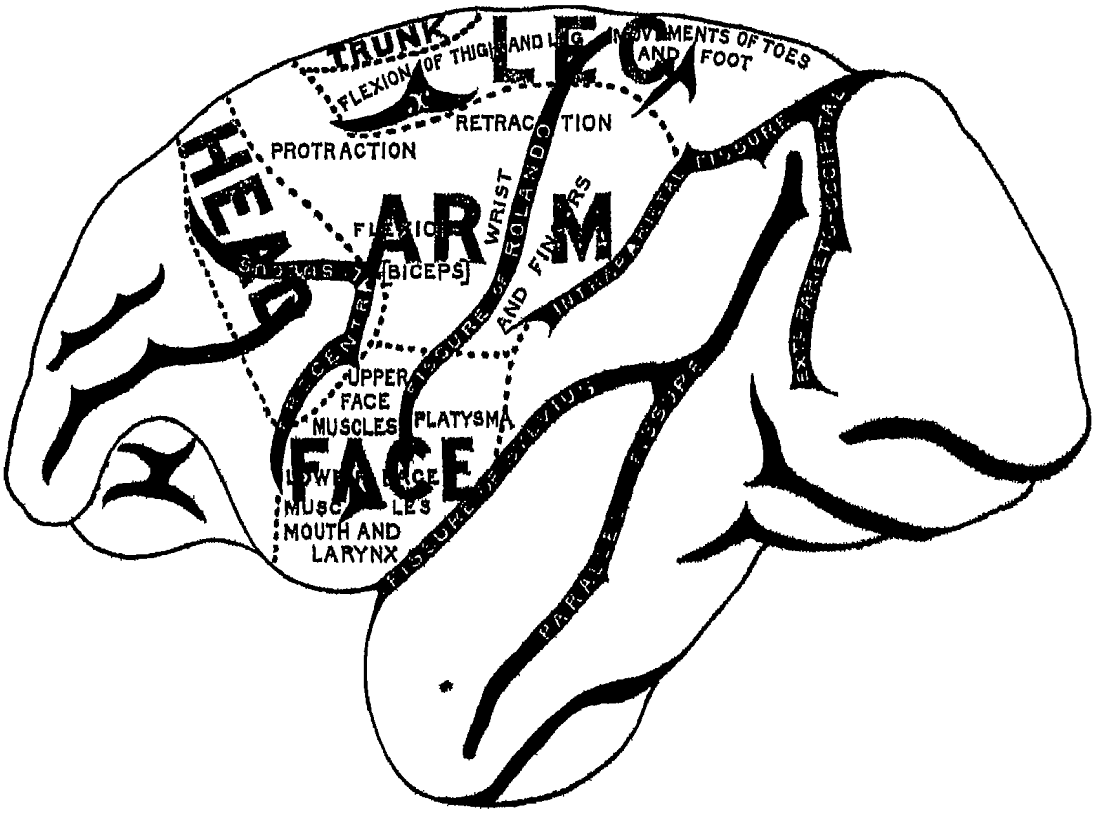
[*] 'Proceedings of the Royal Society,' vol. 23, 1875, p. 409

The *arm-area* occupies a portion of the cerebral surface which is triangular in shape, being broad behind and narrow in front. It comprises most of the upper half of the ascending parietal and ascending frontal gyri, from a little below the level of the sagittal part of the precentral fissure below, nearly to the margin of the hemisphere above, together with the adjacent part of the frontal lobe below the small antero-posterior sulcus marked *x*. In front of this sulcus it bends round to the mesial surface and is continuous with a part of the marginal gyrus, excitation of which also produces movements of the shoulder and arm, and which must therefore be regarded as also belonging to the arm-area.

Diagram I.



Over a large part of this area the actual movement which is obtained is the raising and protraction of the arm and hand, described by FERRIER as resulting from excitation of the area marked (5) in his diagram. In this movement most of the muscles of the shoulder and arm share in some degree or other, the exact part taken by one or other group, and consequently the effect produced, varying with the portion of the area stimulated. As a general fact, it may be stated that the shoulder muscles come into play most strongly when the electrodes are applied near the superior limit of the area, the muscles moving the forearm and wrist when they are applied near the central and inferior portions of the area, and the muscles of the wrist and fingers when applied along the posterior border. Here it is sometimes possible also to differentiate between the different movements of the fingers and wrist, for superiorly the excitation usually produces pronation of the hand with extension of the fingers and wrist, and inferiorly supination of the hand with flexion of the fingers. The production of these movements of the fingers is not confined to excitation of the ascending parietal gyrus,* but in very many cases the same movements are produced by exciting the ascending frontal at the corresponding point just across the fissure of ROLANDO.

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* Although it is convenient for purposes of description to represent the areas and centres of the motor region as if they were sharply marked off from one another, there is no distinct evidence that this is really the case; but, on the contrary, if we are to accept the results of excitation (and, according to LUCIANI, they are confirmed in this particular by the results of localised ablation), there are no such sharp lines of demarcation, but every centre and area overlaps to a greater or less extent the surrounding areas.

† More precise details regarding the character of the movements evoked on excitation of the several parts of each area are given by Professor SCHAFER in an article "Ueber die motorischen Rindencentren des Affengehirns" in 'Beiträge zur Physiologie, C. LUDWIG gewidmet,' Leipzig, 1887.

The supination which frequently accompanies flexion of the fingers on excitation of the lower end of the posterior margin of the arm-area appears to be brought about by contraction of the supinator longus. But just in front of the centre for this movement is a considerable portion of the arm-area, excitation of which is invariably followed by biceps flexion and supination. This may therefore be regarded as a *biceps-centre* (nearly corresponding with that marked (6) by FERRIER†), although other muscles than the biceps are also brought into action when it is stimulated. It includes a portion of the ascending parietal and the adjacent part of the second frontal gyrus, and it abuts below on the face-area, and in front on the head-area.‡ Again the retraction of the shoulder and arm, which is produced by excitation at the upper part of the area on either side of the fissure of ROLANDO, is largely produced, as FERRIER has also shown, by the latissimus dorsi (although other muscles are also thrown into action), and might be described as the *latissimus-centre*.

The *face-area*, although we have so called it for convenience sake, actually gives rise to movements not only of the facial muscles, but also of the whole of the upper part of the alimentary tube (mouth, throat, and larynx). It comprises the whole of the ascending parietal and frontal convolutions below the arm-area, extending down to the fissure of SYLVIUS, and including the external surface of the operculum. It is physiologically remarkable from the fact that many of the movements which result from its excitation are apt to be executed bilaterally, which is only exceptionally the case with excitation of the other areas (except that for the head and eyes).

Excitation of the upper third or half of the area causes winking, or closure of the eyelids, elevation of the ala of the nose, and retraction and elevation of the angle of the mouth. This may be termed the *upper face-centre*.

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* Compare FERRIER, 'Roy. Soc. Proc.,' vol. 23, 1875.

† A lesion of the ascending frontal portion of this centre, producing paralysis of the hand and forearm, is shown by FERRIER in 'Functions of the Brain,' 2nd edition, fig. 113, p 351.

‡ The arm-area has, since our experiments, been carefully investigated by Dr. C. E. BEEVOR in conjunction with Professor HORSLEY. The results at which they have arrived, and which are generally confirmatory of those here given, have been already communicated to the Royal Society.

Excitation over the lower third (*lower face-centre*) is accompanied by varying movements of the jaw and tongue, some of them being very like those of mastication. As a rule excitation of the posterior part of this centre is accompanied by retraction, of the anterior part by protrusion, of the tongue* in combination with movements of the mouth generally. On the other hand, if the electrodes are applied in the middle of the centre, alternate movements of protraction and retraction may be obtained.

At the lower end of the ascending parietal gyrus, and extending in some instances to the lower end of the ascending frontal, is a centre, excitation of which causes the mouth to be opened, accompanied by retraction of the tongue and of the lower lip, and sometimes a bending of the head to the side. This is due to contraction of the platysma myoides. Its action is sometimes produced over a considerable part of the face-area, but always most markedly along that part of the area which lies behind the lower end of the fissure of ROLANDO.†

The *head-area* or *area for visual direction* comprises an oblong portion of the surface of the frontal lobe, extending from the margin of the hemisphere, round which it dips for a short distance, outwards and somewhat backwards to the upper and anterior limit of the face-area. Posteriorly, it is bounded by the arm-area, and in front by the non-excitable portion of the lobe. It extends, therefore, in front as far as the extremity of the precentral sulcus, and it includes the middle part of the frontal lobe above the antero-posterior limb of that sulcus, the part included in the angle formed by the antero-posterior and vertical limbs of the sulcus, and perhaps a small portion of the ascending frontal gyrus, close to the vertical limb of the same fissure. The effects produced by excitation of this area are similar to those described by FERRIER as resulting from excitation of the rather more limited area marked 12 in his diagrams, viz., opening of the eyes, dilatation of the pupils, and turning of the head to the opposite side, with conjugate deviation of the eyes to that side. If the electrodes are applied near the angle of the precentral sulcus, the ears are frequently also strongly retracted.

Besides these three main areas, which occupy the greater part of the excitable region of the external surface, portions of two other areas, one concerned with movements of the lower limb, and the other with movements of the trunk, occupy a part of this surface close to the great longitudinal fissure, although their main parts are found upon the marginal gyrus. The *leg-area* is partly situated upon the mesial surface of the hemisphere, where its limits will be presently pointed out, but it also extends, as we have just explained, over the margin, occupying a strip of the external surface from the parieto-occipital fissure nearly to the level of the anterior end of the small sulcus *x*. In front and externally it approaches the arm-area, and excitation along the line of junction of the two causes the combined forward movement of the arm and leg which FERRIER has described.*

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* As mentioned by FERRIER for his centres (9) and (10), 'Functions of the Brain,' p. 242.

† Since our experiments, Dr. FELIX SEMON, working in conjunction with Professor HORSLEY, has found that the lower end of the ascending frontal gyrus anteriorly is also excitable; an effect being produced upon the glottis by its excitation, viz., to bring about phonatory closure of the vocal cords. A similar centre was discovered in the Dog by H. KRAUSE.

The muscular contractions which are produced by excitation of this strip vary according to the place of application of the electrodes, but they are generally such as to produce flexion of the joints of the lower limb. Behind the upper end of the fissure of ROLANDO the excitation takes effect chiefly upon the ankle and digits, producing most commonly flexion of the foot with either flexion or extension of the digits—most commonly the latter (especially near the posterior extremity of the area). In front of the upper end of that fissure flexion of the foot and movements of the toes are still very common, but the most marked movement is flexion of the leg at the knee, caused by strong contraction of the hamstrings, with the addition, when the electrodes are applied still more anteriorly, of flexion at the hip, so that the whole limb is now brought forward under the abdomen.

The *trunk-area*, unlike the last, scarcely, if at all, extends over the margin to reach the external surface. We have occasionally obtained movements of the trunk when the electrodes have been applied between the sulcus *x* and the margin, but have much more often obtained a negative result as regards the spine and abdominal muscles, movements of the leg at the hip and of the arm at the shoulder being generally the only effect produced. The movements of the tail, which FERRIER describes as being produced by excitations applied over the situation of *x*, we have not obtained at this point.

Results of excitation of the marginal convolution.—As we have already stated in a preliminary communication to the Royal Society,† electrical excitation of the marginal convolution in Monkeys is followed by various movements of the limbs or trunk according to the part stimulated. Excitation of this convolution in the prefrontal region yields no result. But if the electrodes be applied about opposite the anterior end of the corpus callosum, especially close to the margin of the hemisphere, the movement of the head and eyes characteristic of excitation of FERRIER's centre (12) *may* be obtained (extension of the *head-area*, *vide antea*, p. 8, and Diagram II.) A little behind this point well-marked movements of the opposite arm are observed. They occur chiefly at the shoulder, and consist usually of retraction of the scapula and adduction of the arm to the side, but are frequently combined, especially when the electrodes are applied more anteriorly, with movements at the elbow (flexion or extension, more commonly the former), and more rarely with extension of the hand. This portion of the marginal convolution forms, therefore, an extension over to the mesial surface of the hemisphere, of the large *arm-area* of the external surface (*vide antea*, p. 6). Opposite the level of the anterior extremity of *x*, contraction of the muscles moving the upper part of the trunk may be produced, causing a rotation and arching of the dorsal spine (the convexity to the opposite side), but the effect frequently extends also to the lower part of the spine. Superiorly some of the muscles which pass from the spine to the scapula may also be thrown into action, and inferiorly some of those which pass from the pelvis to the lower extremity, especially the glutæi.

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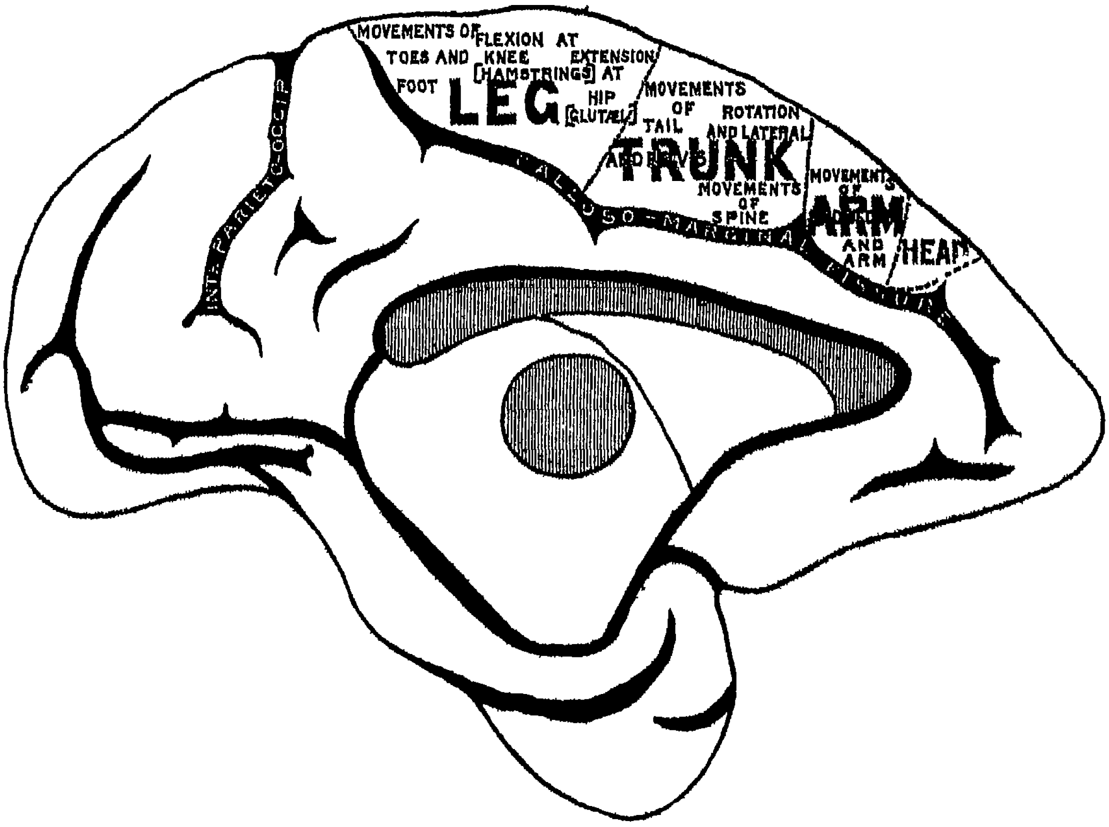
* 'Roy. Soc. Proc.,' vol. 23, 1875.

† HORSLEY and SCHAFER, "Experimental Researches in Cerebral Physiology.—I. The Functions of the Marginal Convolution," 'Proceedings of the Royal Society,' vol. 36, 1884, p. 437.

But the effects upon the lower spine and hip muscles more often result from excitation at a point a little further back, about opposite the posterior end of the furrow *x*. Excitation of this point also almost invariably produces, besides the rotation and arching of the lower spine and the pelvis and extension of the hip, which have just been mentioned, movement of the tail to the opposite side and flexion at the knee, the last-named movement being caused by contraction of the hamstrings.

Diagram II.



At a point slightly farther back, opposite the upper end of the ascending frontal convolution, the flexion of the knee is the most constant result of excitation, but it is often combined with eversion of the foot, and sometimes with flexion of the foot.*

Finally, at the posterior extremity of the convolution, we have usually obtained as the primary result of a weak excitation flexion of the foot and extension of the toes, but other muscles of the leg and foot than those concerned in these movements, and especially the hamstrings, may also be brought into action.

Looking, as a whole, at the results of stimulation of the excitable portion of the marginal gyrus, it would appear that the application of the electrodes at successive points from before backwards produces (1) movements of the head; (2) of the forearm and hand; (3) of the arm at the shoulder; (4) of the upper (dorsal) part of the trunk, (5) of the lower (pelvic) part of the trunk, (6) of the leg at the hip, (7) of the lower leg at the knee, (8) of the foot and toes.* The part which is concerned with the rotation of the head is very small, and close to the margin; it belongs to the large *head-area* of the external surface. The part concerned with movements of the upper limb, which is, as we have already stated, a portion of the *arm-area,* extends back upon the gyrus marginalis to about the level of the anterior end of the sulcus x Then comes a small portion of the convolution, excitation of which is followed by movements of the trunk muscles, causing rotation and arching of the spine. This may be termed the *trunk-area.* It overlaps the arm-area in front and the leg-area behind, and about corresponds in length with the sulcus x, being seldom more than half-an-inch in length. In some cases it appears to extend a short way over the margin towards x. It is certainly not a little remarkable that the numerous and powerful muscles of the spine should be governed from so small a portion of the cerebral cortex, but it is to be remembered that the movements of which the spine is capable are comparatively few and simple. All the rest of the convolution, from about the level of the middle of x to the posterior limit of the gyrus, forms, together with the corresponding strip upon the external surface, the *leg-area.*

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* By "flexion of the foot" dorsal flexion is meant.

In this marginal portion of the leg-area, as in the external portion, we can distinguish between the movements caused by excitation of successive parts from before backwards. When the electrodes are applied to the anterior part the most marked movement usually obtained is at the hip joint, but here it is a movement of extension instead of the flexion produced by excitation of the corresponding part of the external portion of the area. It is usually accompanied by extension or lateral movement of the tail. The movements in question are obviously caused in chief part by the glutæi muscles, and this anterior end of the marginal leg-area may be distinguished as the *glutæus-centre,* but the hamstrings are also usually thrown into contraction at the same time. Next comes a part, opposite the upper end of the ascending frontal gyrus, excitation of which is followed by well-marked action of the hamstrings, either alone or accompanied by contraction of the calf-muscles and peronæi. This is, therefore, an extension of the *hamstring-centre* of the external surface. It overlaps the glutæus-centre in front, and the succeeding centre behind. Lastly, the movements most characteristic of excitation of the posterior part of the area are similar to those caused by excitation of the corresponding part of the external surface, viz., movements of the foot and toes; flexion of the foot and extension of the toes being those which we have most frequently obtained. They are often accompanied by flexion at the knee, due to hamstring action. This part of the leg-area may, therefore, be distinguished as the *foot-centre.*†

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* The movements here mentioned are the primary movements, but, as will be seen from the previous description, they are almost invariably complicated by secondary movements, which are usually the primary movements produced by excitation at the adjacent parts

† The part of the marginal convolution which is concerned with movements of the leg and foot is that portion which is often known as the *paracentral lobule.*

Results of ablation of the external motor areas.—The experiments of FERRIER, both alone and in conjunction with YEO, have yielded distinct and conclusive results from the removal of the excitable areas upon the external surface. But we have found it necessary to repeat some of their experiments partly for the sake of contrasting the effect of removal of these areas with that of removal of those upon the mesial surface; and partly to put to the test the statements of SCHIFF, MUNK, LUCIANI, and other experimental physiologists regarding the sensory functions of these areas.

We have accordingly performed a certain number of experiments involving more or less complete removal of these motor areas, and in some we have at a later period followed this up by removal of the mesial areas as well. In other experiments we have first removed the mesial areas and subsequently those of the external surface. In one or two instances we have cut away the whole of the motor cortex at one operation, but, although the hæmorrhage from this operation need not be excessive, the prostration and shock which accompany the sudden production of such a complete condition of unilateral paralysis* as results from this extensive lesion has in all our cases been so great that the animal has invariably succumbed within a very short period after the operation (seven or eight days at the utmost). The extraordinary degree of shock which accompanies this absolute hemiplegic condition is well exemplified in the case of a large, strong, tame Jew Monkey, from the left side of whose brain had been removed, by three successive operations spread over a period of several months, the occipital lobe, the prefrontal lobe, including a portion of the head-centre, and nearly the whole of the temporo-sphenoidal lobe, including the greater part of the hippocampus major. From all these operations, involving collectively, as they did, the removal of at least one-half of the whole cortex cerebri, recovery was easy and rapid; and, apart from a certain amount of hemiopic disturbance of vision, and a slight degree of facial paralysis (due probably to an accidental lesion in the face-area), was unaccompanied by any permanent symptoms whatever. But on removing the rest of the cortex, comprising the angular gyrus, the motor areas of the external surface, and the gyrus marginalis (but not the gyrus fornicatus), although the amount of brain substance removed was considerably less than in the other operations, the shock and prostration were so severe as to cause death within a few hours. (See 'Record of Experiments,' Case 24.)

The symptoms produced by removal of the external motor areas alone, including that part of the leg-area which extends over the margin, are almost complete paralysis of the opposite arm, facial paralysis, paresis of the leg-muscles, chiefly involving the flexors of the hip and ankle and the extensors of the toes, and greater or less inability to rotate the head to the opposite side. But the trunk-muscles are unaffected, and the paralysis of the lower limb is not sufficiently marked to prevent the animal from using it in the ordinary movements of walking and climbing, although there is distinct and permanent lameness in progression.

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* The hemiplegia which is produced by the complete removal of the whole motor cortex involves not only the limbs and face, but the whole opposite side of the trunk. In speaking of such a hemiplegic condition as distinguished from that which involves only the limbs, we shall in future use the term *complete or absolute hemiplegia.*

We have not performed this ablation bilaterally, nor have we made more than one or two experiments upon the effect of ablations of localised portions of the external surface. Such as we have done, however, afford strong confirmation of the results obtained by electrical excitation. Thus we have found that removal of that part of the ascending parietal gyrus, excitation of which causes movements of the wrist and fingers, is followed by permanent paresis of those parts, the function of no other part of the body being interfered with. And the removal of the arm-area produces paralysis of the opposite arm without any accompanying paresis of face, head, trunk, or leg. Nor does there appear to be any real recovery from the paralysis which may have been produced by the lesion, although in all lesions of the motor areas, when any portion of an area is left, it may happen that the muscles which are governed from that portion may by practice succeed in imperfectly reproducing some of the movements which are ordinarily produced by the paralysed muscles. The effects of ablation of the motor cortex upon sensibility will be referred to later on.

Results of ablation of the marginal gyrus.—The results of *bilateral* ablation of the marginal gyrus from the level of the anterior extremity of the corpus callosum to the posterior termination of the convolution just behind the level of the upper end of the furrow of ROLANDO is, considering the relatively small extent of the cerebral cortex thus destroyed, most remarkable. The operation is followed by complete paralysis of the trunk-muscles, some paresis of the arms, and very extensive paralysis of the muscles of the legs. The paresis of the arms chiefly affects some of the shoulder-muscles, especially those which retract and at the same time elevate the scapula; it is less marked in the case of the muscles of the upper arm and fore-arm, and hardly, if at all, perceptible in those moving the fingers. The paralysis of the leg extends to almost all the muscles, both those which are intrinsic and those which connect the limb with the trunk, with the exception of certain flexors of the hip—probably the iliopsoas and the tensor vaginæ femoris. The attitude and general appearance of a Monkey in which this double lesion has been produced are very striking (fig. 20, Plate 3). Instead of sitting up with back somewhat curved, in the manner normal to Monkeys, an animal which has been submitted to this operation lies prone, with legs and feet outstretched (or at most with flexed hips), back flat, tail straight and motionless, and arms put forward to clutch at any neighbouring object. The head retains its power of rotation as well as flexion and extension, and the movements of the eyes and facial muscles appear normal. The animal frequently props itself upon its elbows, but never assumes the normal sitting attitude. If the Monkey desires to sit up, it can only do so by dragging itself into the sitting posture by its arms and hands, and holding on by these to the wires of the cage or to any neighbouring object. If the hold be detached, the animal immediately tends to fall over. Progression is effected almost entirely by the arms, the Monkey dragging itself along with the aid of these, assisted by the flexion which occurs at the hips; the legs are quite limp and draggled, the dorsal surface of the toes being drawn over the ground.

This ablation, although involving a more limited removal of the skull-cap, and a smaller cerebral injury than almost any other operations that we have undertaken, and although it can be performed with very little hæmorrhage and disturbance of the cerebral circulation (for the veins which are passing from the external surface to the longitudinal sinus can generally be avoided without the necessity of cutting or tying them), is nevertheless followed by much more considerable shock than any other lesion, even of much greater extent. Indeed it is difficult to keep an animal, on which the bilateral operation has been performed, alive for more than a few days, even although it may be got to feed fairly well, for diarrhœa is apt to supervene, and the animal soon gets emaciated and dies. Out of four cases in which we have performed the bilateral operation at one sitting, two died, in spite of every care, on the eighth day, and the other two survived only three or four weeks. But even in these last cases there was no recovery from the paralysis, although the animals learned to get about and even to climb the wires of the cage quite readily with the use of their arms, the legs being always used merely passively as props.

The results which follow *unilateral* removal of the gyrus marginalis are perfectly well marked, but far less striking. This arises from the fact that the animal is able to assume and maintain a nearly normal attitude; a result due, no doubt, to the action of the muscles upon the one side of the spine being sufficient for this purpose. Rotation of the trunk to the side opposite to the cerebral lesion appears, however, to be deficient, and paralysis of the opposite leg is always very distinct; the foot and leg hanging down when the animal is seated upon a perch, and remaining passive when the animal is taken up by the shoulders and somewhat rapidly lowered to the ground. Under these circumstances a normal Monkey will always extend the hip and put down the foot to meet the ground, but in cases with a unilateral lesion of this description it is only the foot which is upon the same side as the cerebral lesion which is thus lowered. The hip can, however, be freely flexed, and the paralysis of the leg-muscles does not appear to be nearly so well marked when only one side is involved as it is after the performance of the double operation. Indeed, while the animal has been running and climbing, it is difficult to distinguish the paralysed side. It is certain that such constantly recurring actions as walking and running, to which, in the case of the Monkey, we may add climbing, may by habit almost cease to lose their distinctively voluntary character, and it is conceivable that they may be often carried on by the action of the lower nerve-centres in the cord and medulla oblongata after having been started by that of the higher centres in the cerebral cortex. But it must be admitted that when the paralysis of any true voluntary movement which has been produced by ablation of a part of the cerebral cortex is complete and extensive it is in most cases not followed by recovery ; and it is not impossible that in those instances in which recovery seems to occur the permanent injury has been less complete than was at first supposed from the effects exhibited, but has been temporarily extended by the disturbance produced in the neighbouring grey matter by the operation.

We have performed the operation of removing the grey matter of the gyrus marginalis of one side of the brain, at least of its posterior two-thirds or more, in eight cases, and in some of these, after a lapse of time, varying from a few days to several weeks, it was followed by a second operation for the removal of some other portion of the motor cortex.

Conclusions and remarks.—The results of ablation in the motor regions of the cortex afford very direct corroborative evidence regarding the functions of those regions which are deducible from the effects of excitation. This is already perfectly well known so far as regards the areas of FERRIER upon the external surface, and our experiments on the ablation of these areas are so far only confirmatory of those of previous observers. They show, however, in addition, that in order that the hemiplegia or paraplegia which is produced by cortical ablation shall be complete it is necessary to include the part of the marginal gyrus corresponding in longitudinal extent to the excitable areas of the external surface, and indeed that the amount of paralysis produced by ablation of the marginal gyri alone is as great as, or even greater than, that caused by removal of the much more extensive external areas. But, on the other hand, the *complexity of the muscular movements* which are governed from these areas, including as they do most of the movements of the arm and fingers, and of the face and head, is evidently much greater than in those which are governed from the marginal gyrus.

Effects of ablation of the excitable areas of the cortex upon sensibility.—It is much more difficult than would at first sight appear to determine in animals whether a part in which motor paralysis has been produced by a lesion of the cerebral cortex is deficient in sensibility. For, on the one hand, the subject of the experiment no longer possesses the power of voluntarily withdrawing the irritated part, and thus the most obvious indication of perception of sensation is necessarily absent, while, on the other hand, there is the possibility of an involuntary or reflex response which might without due care be taken to indicate the continued existence of sensibility It is, however, undoubtedly the fact that in our cases of cerebral lesion producing paralysis of voluntary motion reflex movements of the paralysed part are produced with great difficulty and require a powerful stimulus; from which it would appear that the inhibitory action exercised by the brain over reflex movements is not only not removed by a lesion of the cortex which is accompanied by loss of power voluntarily to produce contraction of the muscles, but is on the contrary markedly increased by such lesion.

We have seen sufficient, however, to convince ourselves that a lesion of the cortex which produces paralysis of voluntary motion in a part is not necessarily accompanied also by loss of general sensibility of the paralysed part. At the same time there is often undoubted diminution of reaction to stimuli of various kinds (touch, prick, hot wire, electric shocks), but it is impossible to say how far this may indicate a corresponding diminution of sensibility. Monkeys present very great differences in the degree to which they exhibit emotion, some being habitually dull and stupid, while others are lively and mercurial in temperament. In those belonging to the former class it is often difficult to elicit any information from the expression of the face, so that an irritation of the paralysed limb, insufficient to cause general movement of the body, does not provoke any indication of perception. On the other hand, in lively Monkeys we have often obtained, as the result of even slight irritation of paralysed parts, unmistakable signs of perception, and in cases of this kind in animals one positive observation must be regarded as of greater importance than many negative statements. But in dealing with questions of sensibility the results of experiments upon animals must always be to a certain extent unsatisfactory, since we can obtain no evidence of the actual character of the sensation provoked. Fortunately it is probable that the elucidation of this question by careful observations of cases of cerebral injury in Man will not long be wanting

Difficult as it is to decide in animals questions relating to the general and tactile sensibility of a limb deprived of voluntary motion, it is yet more difficult to form any opinion regarding the presence or absence of the so-called muscular sense. It was the opinion of HITZIG that a lesion of the motor cortex effected an abolition of the muscular sense of the part paralysed, and he inclined to regard the paralysis as produced rather in consequence of the loss of this directive sensation than immediately by removal of motor nerve-cells. This mode of viewing the question and of explaining the facts of experiment has been adopted and ably advocated by BASTIAN, who brings forward a large amount of evidence derived from pathological observation in its favour.* FERRIER, on the other hand, appears to admit only the direct production of motor paralysis, and is disposed to localise all kinds of sensibility, including the muscular sense (which he regards as entirely derived from indications conveyed by nerves of ordinary tactile sensibility) in other regions of the cortex than those connected with the production of voluntary motion; while others, again, amongst whom SCHIFF and MUNK are to be included, endeavour to show that, while from one set of nerve-cells of the excitable regions of the cortex the fibres which convey voluntary impressions may directly arise, other cells of the same regions, indirectly connected with the first set, may serve as the terminal organs of the nerve-fibres, which convey sensory impressions, general, tactile, and muscular, and may transfer these centrifugal impressions to cells which give origin to the fibres of the motor tract. And it would appear that, in connection with this view, those who advocate it are for the most part of opinion that it is the superficial layers of smaller cells of the grey cortex that are immediately connected with the sensory tracts, and the larger cells of the deeper layers of the cortex that give origin to the fibres of the motor tract.

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* 'Brain as an Organ of Mind.' See also his article on Motor Centres and the Muscular Sense in a recent number of 'Brain.'

In order to test this last opinion, we in one instance endeavoured to destroy, by searing the surface of the excitable region of the brain with the actual cautery, the superficial part of the grey matter, while leaving the deeper layers of nerve-cells intact. In spite of the complete blocking of the superficial vessels which is produced by this treatment, we obtained only an incomplete muscular paralysis as the immediate result of the operation, but, although the superficial layers of the cortex must have been destroyed, there was no diminution of sensibility in the parts affected by paresis The subsequent softening and disintegration which occurred in consequence of the thromboses caused by the cautery was accompanied by a much more complete condition of muscular paralysis, but the general sensibility of the opposite side was still apparently unaffected, and continued so until the death of the animal (see 'Record of Experiments,' Case 6, and fig 6, Plate 1)

The result of this experiment, so far as it goes, is opposed to the opinion in question, but we would disclaim attaching too much importance to a single case of the kind, especially since the depth of the primary lesion could not have been uniform, and was probably much less in some parts than in others. It must be admitted that the question whether there is any localisation of sensibility, either for the muscles which are governed from the cortical motor regions or for the parts which they move, is one which can scarcely be answered by experiments upon animals, and that for its solution we must await the result of clinical and pathological observation upon Man.*

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* H MUNK ('Ueber die Functionen der Grosshirnrinde, 4te Mittheilung,' fig 4, p 63) has mapped out the external surface of the Monkey's brain in a manner which, in certain particulars, corresponds with the plan we have here given (in Diagram I) Although he regards the areas in question as sensory rather than motor, the difference is merely one of terms, for the facts upon which he rests this opinion are nearly the same as those which have guided us in arriving at our results. For the author (p 66) admits that he has found it difficult to prove that after extirpation of his so-called "sensory areas" in Monkeys there is any loss of sensibility, at least to pressure, and it seems to be a mere assumption that other forms of sensation, such as tactile sensibility and the muscular sense, are abolished Dismissing, then, the question of nomenclature, the two plans, so far as they deal with the same regions, are strictly comparable

On instituting such comparison, we find that our *leg-*, *arm-* and *face-areas* very nearly correspond with those of MUNK (who, however, designates as *head-region* that which we term the *face area*, but connects it with the movements of the same parts as our *face-area* is concerned with) The main differences are to be found in the other two areas, viz, those for the trunk and head and eye movements respectively MUNK's *trunk region* occupies the prefrontal lobe, whilst our *trunk-area* is comprised within the *leg-region* of MUNK We have already given our reasons for believing that MUNK is altogether mistaken in believing that the prefrontal region is concerned with movements of the trunk The area concerned with rotation and lateral movements of the head, which MUNK designates the *neck-region*, appears far smaller than the corresponding area in our plan, and even much smaller than that given by FERRIER

III.—LESIONS OF THE OCCIPITAL LOBES.

We have found that removal of the occipital lobe upon one side is followed, as MUNK[*] was the first to prove, by a condition of hemiopia; blindness being produced in the lateral half of each retina corresponding to the side of the brain which has been submitted to the operation The blindness is at first complete. The animal takes no notice of a threatened blow directed from the opposite side, tends to knock against obstacles which lie in the way of that side, and only picks up such objects (raisins, &c) as happen to lie upon the same side of the mesial plane of vision. In a few days, however, this condition begins to pass off· threats are avoided; large objects lying on the opposite side of the mesial plane are seen and picked up, at first with some awkwardness, and eventually it is not possible to substantiate any permanent affection of vision. We have performed this operation four times. We have removed the occipital lobes of both sides in two cases only, and in these by two successive operations, only a short interval of time having elapsed between them; one only of these two cases survived the operation for any length of time. At first complete blindness, affecting the whole visual field, was the result, but this appeared to be subsequently in great measure recovered from, although it seemed to us that there was some permanent impairment of visual perception. For, although objects were undoubtedly seen, there was much greater slowness and difficulty manifested in seizing them. This was the case at least with such a small object as a currant upon the floor, the animal often fumbling about for a moment or two in the attempt to pick it up. More conspicuous objects did not appear to offer the same difficulty, for the animal would spring from the side of the cage on to a hanging rope with unerring precision.

In this case, in which we had removed both occipital lobes in previous operations, and after the animal had recovered its visual perceptions so far as has just been described, we subsequently cut away the cortex of the angular gyrus of one side. This lesion was followed by a return of hemiopia, which remained permanent and apparently complete until the death of the animal (from dysentery) four months later. This is the only experiment we have made upon the angular gyrus. We have also sometimes produced hemiopia in consequence of operations involving the under-surface of the temporo-sphenoidal lobe. These cases are probably to be explained by the fact that the optic radiations into the occipital lobe have been reached by the

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Movements of the eyes MUNK appears inclined, but on very insufficient grounds, as it seems to us, to connect with the angular gyrus. The *ear-region* he places around the extremity of the SYLVIAN fissure.

It must be borne in mind that the plan which MUNK has drawn up has been obtained chiefly, if not entirely, by ablation, whereas ours is mainly the result of excitation. Unfortunately MUNK has not given the particulars of his experiments, but has merely stated their general tendency. In our opinion their value would be greatly enhanced, were the precise symptoms manifested during life, and the exact extent of the cortical lesion in each case, as determined by post-mortem investigation, recorded.

[*] 'Functionen der Grosshirnrinde—Erste Mittheilung.' 1877.

lesion * In one or two of these instances there has occurred softening of the occipital lobe, at least of its lower part, probably in consequence of derangement of its vascular supply.

Conclusions and remarks.—Our experiments upon the occipital region, although few in number, seem to link together the conclusions arrived at by MUNK, and by FERRIER and YEO, as the result of their experiments. They indicate that both the occipital lobes and angular gyri are concerned with visual perceptions in such a manner that each occipital region is connected with the corresponding lateral half of each retina, and that a part only of the cortex of the region in question is able to take on in great measure, how completely cannot be determined in animals, the functions of the whole This is in conformity also with the results of LUCIANI. So far as the occipital lobe alone is concerned, our observations confirm the statement of MUNK that the effect of this lesion is to produce a hemiopic disturbance of visual consciousness. But the imperfect vision which remains after removal of both occipital lobes (see Cases 25 and 26) suggests that the area which is concerned with visual consciousness is not confined to those lobes, as was inferred by MUNK, but extends over into the angular gyrus, permanent hemiopia being produced by the subsequent removal of that convolution. It will, however, be necessary that further experiments should be undertaken in order to determine more precisely, not only the extent, but also the relative importance of the anterior, posterior, and mesial portions of the visual area of the cortex †

IV.—RESULTS OF EXPERIMENTS UPON THE TEMPORO-SPHENOIDAL LOBE AND ON THE LIMBIC LOBE.

We have in several instances effected the removal of the greater part of the temporo-sphenoidal lobe. Our object in most of these experiments was to get at the hippocampal region in order to remove or destroy the hippocampus and uncinate gyrus, a lesion which had only been performed hitherto by FERRIER, partly in conjunction with YEO, and which in the hands of those observers was followed by hemianæsthesia more or less complete.* But, as their experiments were performed by a less exact method than that of simple excision, and since moreover in none of their experiments upon this region did the animals survive more than a few days, it occurred to us to approach the same part from the outer side after removal of the lateral portion of the temporo-sphenoidal lobe, instead of from behind through the occipital lobe, and we accordingly endeavoured in the first instance to determine what effect, if any, is obtained by removal of this portion. Our results have proved uniformly negative so far as the larger portion of the lobe is concerned. The animals have exhibited no signs of motor paralysis nor any loss of general or tactile sensibility.† We have usually left the whole or part of the superior temporo-sphenoidal gyrus and the anterior extremity of the lobe, but in one of our cases the superior gyrus was almost completely removed upon both sides, only the narrow posterior extremity, for about $\frac{3}{8}$-inch in length, being left upon the right side. In this case the animal certainly appeared to hear quite distinctly, and so far as it goes the experiment is at variance both with the results of FERRIER and with those of MUNK. But we have not as yet systematically pursued the question of the cortical localisation of auditory sensations, although it is right to state that such incidental observations as we were able to make upon this function have almost uniformly proved negative.‡ We have not, as the result of any bilateral operation, been able to convince ourselves that deafness has been established in a single case.§ This is indeed a very difficult point to determine in many intact Monkeys, which, when their attention is attracted by other causes, will often fail to give evidence of the hearing even of loud noises, while, on the other hand, other individuals readily show that they are conscious of the slightest unusual sound.

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* LUCIANI ("On the Sensorial Localisations in the Cortex Cerebri," 'Brain,' vol. 7) appears disposed to regard these cases as being due to injury of an extension of the visual region into the temporal lobe But, since the main centre for vision (in the occipital lobe) is intact, one would scarcely expect hemiopia to result from the removal of an outlying part!

† A further investigation upon this region and into the parts of the cortex which are connected with other special sense functions is, in fact, now being carried on by one of us, in the hope of succeeding in clearing up some of the discrepancies in the evidence of previous observers We may perhaps here most conveniently notice a statement which has been made by Dr. FERRIER in the second edition of his 'Functions of the Brain,' to the effect that we had removed the occipital lobes on one or both sides "without the slightest appreciable impairment of vision." It will be seen from the text, and from our Record of Cases, that this is a mistake. It appears to have arisen solely from a misunderstanding, for, whereas we informed Dr. FERRIER that we had not been able to determine that this lesion produced any *permanent* impairment of vision, he understood, it would seem, that we had not obtained any effect whatever.

In our earlier experiments upon the hippocampal region we were satisfied, after removing the external part of the temporo-sphenoidal lobe, and exposing the hippocampus major by opening up the descending cornu of the lateral ventricle, with removing as much of the hippocampus major as could conveniently be got at, usually about three-quarters of an inch, and the adjoining portion of the uncinate convolution. Such removal, although effecting an extensive lesion in this region, produced, however, no effect, so far as we could determine, upon the sensibility of the opposite side of the body, such as we had been led to expect from the experiments of FERRIER would have been the case On communicating this result to Professor FERRIER, he suggested that the difference probably arose from the smaller extent of the lesion, especially of the uncinate gyrus, as compared with the cases published by him, and we accordingly in further experiments endeavoured to effect a more complete removal of that convolution as well as of the hippocampus itself. The result of this was that in many cases there was produced, as FERRIER has described, a unilateral diminution of sensibility affecting the whole of the opposite side of the body. This condition of hemianæsthesia, although fairly well marked, was in our experiments never complete, nor was it permanent, and, indeed, in most instances it was found to have disappeared within a week of the operation Since even with a tolerably extensive lesion in this region we were not always able to substantiate the fact that there was a diminution of sensibility produced, at least on testing the animals some hours after the operation, and since also, when a distinct effect was obtained, it was comparatively transient, it was difficult to be certain that the result yielded by the operation was really due to the removal of a part of the cortex connected with the consciousness of sensations, and might not be otherwise explained, as we have previously pointed out, by a disturbance of the function of other parts, which must always be produced by any extensive cerebral lesion; and this explanation seems at all events as reasonable as one which assumes that it is exclusively the region in question which is concerned with the appreciation of tactile and painful sensibility. Another explanation is, however, possible, and would equally well fit in with the facts which we have to record. For, as we shall immediately show, the gyrus fornicatus is certainly connected with the sensibility of the opposite side of the body. Now the gyrus fornicatus is anatomically to be regarded as a direct continuation of the gyrus hippocampi (the two constituting the great limbic lobe of BROCA).* It is probable, therefore, that the functions of the two are similar, and possible that, as in the case of the visual sensory area, after removal of a part, the remainder of the area can carry on, more or less efficiently, the functions of the whole. But, before discussing this possibility further, we will describe the results we have obtained from lesions of the gyrus fornicatus.

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* FERRIER, 'Phil. Trans.,' 1875, and 'Functions of the Brain,' pp 327 *et seq.* FERRIER and YEO, 'Phil. Trans.,' 1884.

† That is, after the shock of the operation was recovered from.

‡ Dr. FERRIER is mistaken in the statement ('Functions of the Brain,' 2nd edition, pp. 310, 311) that we have been able to corroborate his observations upon the localisation of this function in the superior temporo-sphenoidal gyrus in Monkeys We have so far neither obtained any distinct corroboration nor refutation of them, but regard the question as still open, and, as we have stated in a preceding note, one of us is now engaged in a further investigation regarding the localisation of this and other special sense functions. The same statement will also hold good with regard to the localisation of olfactory and gustatory sensations. Unilateral lesions are probably of but little value in elucidating these functions; at least, we have been unable to obtain any determinate results from them.

§ It is right to add that we were not specially intending to investigate this point (the localisation of auditory perceptions), and that the lesions of this lobe which we record were performed with another object, viz., to arrive at the hippocampal region. But, as we have been careful to note all the symptoms that we could observe, they are not without their value on this point

Experiments upon the gyrus fornicatus.—We have endeavoured to remove the cortex of the gyrus fornicatus by exposing freely the upper surface of the hemisphere, drawing the brain gently away from the falx with retractors, and bringing to view the convolution in question, which could thus, with some difficulty it must be admitted, be got at and cut away to a greater or less extent by the aid of a specially constructed curved knive. We have operated in this way upon the gyrus fornicatus in a number of Monkeys, and, although we have never succeeded in effecting a complete removal of the grey matter of the convolution—indeed, from the depth at which it is situated this is scarcely possible without injuring neighbouring parts or producing fatal hæmorrhage—we have in several instances removed or destroyed considerable portions without lesion to other parts, or with but a small injury to the marginal gyrus, the effect of which, from our previous experiments upon this region, could be readily discounted As the result of these experiments, we have found that any extensive lesion of the gyrus fornicatus is followed by hemianæsthesia more or less marked and persistent. In some cases the anæsthetic condition has involved almost the whole of the opposite side of the body, in others it has been localised to either the upper or the lower limb and to particular parts of the trunk, but we have not yet succeeded in establishing the relationship between special regions of the body and the parts of the convolution which have been destroyed. Moreover, the anæsthesia was frequently very pronounced and general during the first three or four days after the operation (and indeed in several instances took the form of complete insensibility to both tactile and painful impressions, so that even a sharp prick or the contact of a hot iron would produce no indication of sensation), but after that time this general condition would become gradually in great part recovered from, or more localised in definite regions. In all cases, however, in which the diminution of sensibility was well marked during the first few days, it has persisted, although with lessened intensity, for many weeks in those instances in which the animals have been preserved for so long. In other cases, in which apparently the lesion was slight, the diminution of sensibility, although at first well marked, subsequently disappeared entirely. In some instances the hemianæsthesia took the form of inability (or a diminution of ability) to localise the seat of irritation, whilst in one case, in which diminution of sensibility was exhibited in a very striking manner, the irritation, when rendered sufficiently intense for the Monkey to become conscious of it, was responded to by the animal scratching a different part of its body from that to which the stimulus was applied.

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* In the Kangaroo, as BEEVOR has shown, the microscopic structure is identical in both the gyrus fornicatus and gyrus hippocampi

These experiments were frequently, but by no means in every case, complicated by the presence of a certain amount of motor paralysis, chiefly, if not entirely, affecting the muscles of the leg. We have no doubt that this condition was always due to a lesion (accidentally produced during the operation, or subsequently, as the [illegible] interference with the circulation) in the leg-area of the marginal convolution. [illegible] of these cases the anæsthesia affected chiefly the paresed limb, and [illegible] argued by those who, like SCHIFF and MUNK, hold that the [illegible] are concerned with the perception of sensory impressions [illegible] the body that the loss of sensibility was due to [illegible] against this argument we may not only put [illegible] has been no accompanying paralysis, but [illegible] well marked in [illegible] limb and upper part of the trunk, while the lower (paresed) limb has exhibited no diminution of sensibility whatever.

We have performed a few experiments in which we endeavoured completely to destroy, upon the same side of the brain in successive operations, both the hippocampal convolution and the gyrus fornicatus, *i.e.*, the whole of the limbic lobe. Although we cannot claim to have fully succeeded as yet in this attempt, having been foiled by the extreme difficulty of getting at all portions of this lobe, our results have not been devoid of interest. They have tended to show that, while a lesion of either the hippocampal gyrus or of the gyrus fornicatus alone produces, as the experiments of FERRIER have shown for the former convolution—and our own, just alluded to, for the latter—a more or less marked diminution in the power of appreciation of sensory impressions applied to the opposite side of the body, the part played by the gyrus fornicatus is of greater importance in this respect than that played by the hippocampal convolution and hippocampus. For when even a considerable lesion has been made in the hippocampal region the resulting hemianæsthesia is not always very well marked and is not long persistent. If, however, this is now followed by an extensive lesion of the gyrus fornicatus, the hemianæsthesia is very well marked and long persistent. On the other hand, when the operation has first been performed upon the gyrus fornicatus, the anæsthetic condition is, as we have seen, very well marked if the lesion has been considerable, and persists in a diminished form for an indefinite period And a lesion of the hippocampal region will now produce but little increase of the anæsthesia. From which it would appear that, although the whole limbic lobe may be concerned in the perception of sensory impressions, the part played by the gyrus fornicatus, at least as respects cutaneous sensibility, is more important than that played by the hippocampal portion of the lobe. But until it has been possible entirely to destroy the whole lobe upon both sides of the brain it is impossible to determine whether it is assisted in its function by any other portion of the cerebral cortex.*

Conclusions and remarks.—The results of our experiments upon the limbic lobe seem to point to the conclusion that this portion of the cerebral cortex is largely, if not exclusively, concerned in the appreciation of sensations, painful and tactile. This is an extension of the view put forward by FERRIER, who was inclined, as the result of his own experiments, to limit that function to the hippocampal region. Dr. FERRIER, who was good enough to assist at some of our experiments upon this part, has fully accepted the conclusions to which they point.† These conclusions appear, however, completely incompatible with the views of most of our predecessors in the field of experimental cerebral research. Of these predecessors we need now refer only to GOLTZ, SCHIFF, and MUNK. With reference to the views of GOLTZ, we may remark that the evidence of the exact localisation, in a particular region—and that a comparatively limited one—of the cerebral cortex, of a function so universally distributed over the body as common sensation, affords the strongest corroboration of the evidence already accumulated on the question of cerebral localisation by the demonstration of the localisation of speech, of voluntary motions, and of certain special sense functions in particular parts—all of which has tended to show that, in the higher vertebrates at least, such localisation of cerebral function is carried out to a remarkable and, previously to the experiments of FRITSCH and HITZIG, an entirely unsuspected extent.

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* It is important here to remark that the possibility of an accidental lesion of the ascending sensory tracts, which has sometimes been put forward as an objection to the anæsthesia obtained by FERRIER from lesions in the hippocampal region, is altogether absent in the case of a lesion of the gyrus fornicatus.

† 'Functions of the Brain,' 2nd edition, pp. 341 *et seq.*

As for the view, originally put forth by SCHIFF and extended by H. MUNK, which has been already referred to (p. 16), we would merely now point out that, although this portion of our researches cannot be said to have directly disproved MUNK'S hypothesis, it must yet be admitted that it has rendered that idea unnecessary. For, as we have already endeavoured to show, the only evidence in favour of MUNK'S view is the slowness of reaction of a paresed part, and this slowness of reaction may be explained otherwise than by the assumption of a defect in sensibility. But if without any muscular paresis we can obtain by a definite and localised lesion complete tactile anæsthesia of a limb, while by a lesion in a different part of the cortex we can produce complete muscular paralysis without any perceptible anæsthesia, the conclusion that the part of the brain involved in the first lesion is alone concerned with the appreciation of sensibility in that limb, to the exclusion of the part involved in the second lesion, seems logically irresistible.

RECORD OF CASES. (See Plates 1–7.*)

1.

Lesion.—Removal of the prefrontal part of the brain (anterior fourth of frontal lobes) on both sides at one operation.

This animal was kept alive five months, during which time no abnormal symptoms of any kind were noticeable. Careful testing showed no apparent deficiency of sensibility. The animal seemed lively and intelligent throughout.

The brain is represented, as seen from above, in fig. 1, Plate 1.

2.

Lesion.—Complete removal of prefrontal region on both sides by vertical incision. [illegible] extended a little further back than in the preceding case. The orbital [illegible] in the removal, but the olfactory tracts were left.

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* [illegible] the post-mortem condition of the brain in each case is represented with [illegible] lesion marked out by darker shading. The numbers attached to [illegible] of the cases in the Record. In some instances sections of the [illegible] Most of the drawings were made for us by [illegible] and we can answer for their fidelity. [illegible] have deposited in the Museum of

Result.—No perceptible permanent symptoms were produced.

This animal was kept nearly three months.

The brain is represented in fig. 2, Plate 1, as seen from above.

3.

Lesion.—The same as in the previous case.

This animal did not properly recover from the result of the operation, for death was caused on the sixth day apparently by compression of brain from accumulated serous fluid. Up to the fourth day no abnormal symptoms were presented (with the exception of the peculiar attitude before mentioned as characteristic of these lesions (p. 3), which was exhibited also for the first few days by Monkeys 1 and 2).

The brain is represented in fig 3, Plate 1, as seen from above.

Lesion.—Left ascending frontal and ascending parietal gyri removed by galvanic cautery,[*] except the lowermost part. The ablation includes also most of the parietal lobule and a part of the superior frontal convolution.

Result.[†]—Right arm is kept flexed at elbow, and adducted and rotated forwards at shoulder.[‡] Hand hangs down with fingers nearly straight, no movements of hand. Slight movement possible at elbow (re-flexion after being straightened) and at shoulder joint. Right leg is kept flexed at hip, knee, and ankle; some amount of movement is possible at all these joints. Toes remain semiflexed It is difficult to detect facial paralysis, but the right cheek pouch cannot be emptied without the assistance of the hand or by being pressed against the shoulder. No paralysis of trunk perceptible. No impairment or paralysis of head-movements was noticed. Lived four months after operation. Death from diarrhœa.

The brain of this Monkey is shown in fig. 4, Plate 1.

5.

Lesion.—Of very nearly the same character and extent as in 4, but upon the right side of the brain.

The *symptoms produced* were almost exactly the same as in 4, except that there was much less paresis of the leg-movements. When in active motion, all four limbs may occasionally be used, but the movements of the left arm are very imperfect, and ordinarily this limb remains flexed and motionless. The hand and fingers are paralysed. Very little, if any, paresis of face-muscles. No paresis of trunk or of head-movements was detected.

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[*] In this and a few other experiments the cautery was used to effect the removal of the cerebral substance. In all other cases we simply cut the part away with a sharp knife.

[†] In all cases, unless otherwise expressly stated, the symptoms which are given are those which are manifested after recovery from the immediate effects of the operation and complete healing of the wound involved in performing it. In all cases also it may be assumed that the symptoms persisted until the death of the animal, unless the contrary is noted.

[‡] This position may have been due to contracture.

Lived two months after operation. Cause of death doubtful; probably chill. In this Monkey the lesion was found on post-mortem examination to involve a strip of the angular gyrus, but no symptoms affecting visual perceptions were noticed during life.

The condition of the brain is shown in fig. 5 as seen from above, and in fig. 5A as shown in section, the section passing through the middle of the lesion. It is seen from the section that the whole thickness of the grey matter was completely removed over the area operated upon. Just at this point the marginal gyrus is somewhat encroached upon by the cut made into the white matter, but in other parts it was not touched.

6.

Lesion.—In this Monkey the motor region of the external surface on the left side was touched quite superficially with the actual cautery.

Result.—The motor paralysis for the first three or four days was not nearly so complete as after excision or deep cauterisation, but afterwards became more complete. There was no perceptible difference of sensibility on the two sides of the body.

The animal only survived the operation a few days. After death the grey matter under the cauterised surface was found to be considerably disorganised, and sections through the hemisphere revealed the presence of numerous infarcts in the subjacent white substance.

The brain is represented as seen from above in fig. 6, Plate 1, and in section through the lesion in fig. 6A.

7.

Lesion.—The whole of FERRIER's areas in front of the fissure of ROLANDO were removed in this Monkey, the lesion extending nearly to the margin above, as far as the fissure of ROLANDO behind, and in front and below as far as an oblique line connecting the antero-superior extremity of the precentral sulcus with the lower end of the ascending frontal gyrus.

[illegible]—The only symptom exhibited up to the 7th day after the operation, *i.e.*, [illegible] occurrence of the unfavourable conditions mentioned below, was [illegible] muscles below the shoulder, without contracture. No [illegible] the trunk, leg, or in the face.

[illegible] day, when the skin began to slough, [illegible] day. This [illegible] prevented [illegible]

Lesions.—In this animal a lesion had been established in the posterior part of the gyrus fornicatus on the right side, but the Monkey was at first so wild that no definite result could be obtained regarding loss of sensibility It was therefore determined to employ it for an operation upon the motor region, and accordingly sixteen days after the first operation a lesion was effected in this part. The lesion consisted in the removal of the greater part of the motor area of the external surface on the right side.

Result —The result of this second lesion was to cause paralysis of the left arm and paresis of the leg, with the exception of the extensor muscles of the thigh, which acted normally.

Experiments upon the sensibility of the left side were again tried, but again with very unsatisfactory results. Sometimes there was no movement caused by a stimulus applied to that side, when there would be marked movement produced on applying the same stimulus to the right side, but, on the other hand, this may well have been the result of the establishment of the motor paralysis, for on stimulation of the left side the animal, without moving away, would occasionally exhibit dissatisfaction by squeaking.

The paralysed condition was maintained until the animal was killed three-and-a-half months after the second operation.

The brain is represented in fig. 8, Plate 1.

9.

Lesion.—Excision of the middle two-thirds of the left ascending parietal gyrus, including a small portion of the parietal lobule.

Result.—The only result produced by this lesion was paresis of the fingers of the opposite hand, power of both flexion and extension being diminished.

The animal was kept two months after the operation.

The brain is represented in fig. 9, Plate 1.

10.

Lesion.—Complete removal of posterior two-thirds of right marginal gyrus.

Result.—Left foot paralysed ; the toes opposed, semi-flexed, and with hallux turned under them. Hamstrings are almost completely paralysed , also glutæi, extension of hip being very feeble. In standing and leaping, the right leg is almost exclusively used ; when lowered towards the ground, puts down right leg, never left. Can *flex* left leg and even manage to scratch left side of trunk with it, but to scratch the left side of the neck the right hand is used. The tail tends to lie over on the right side. No other paresis observable. Can advance and flex left arm and grasp well with fingers of left hand. Can turn head to left.

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* Exhibited to the Neurological Society.

This animal lived three months. The brain was unfortunately mislaid, so that we are unable to give a representation of it, but the exact extent of the lesion had been carefully noted at the time of operation.

11.

Lesion.—Removal of a longitudinal strip of grey matter on the left side of the brain along the margin of the longitudinal fissure from the anterior end of the precentral sulcus nearly to the parieto-occipital fissure.

Result.—The day after the operation there was some paralysis of both right limbs, with unsteadiness of gait. The arm, however, after a few days recovered to all appearance completely. But in the leg, although it was difficult after a time, when the animal was freely running and climbing, to obtain evidence of paralysis, yet when sitting on a perch the right leg always hangs down, and when the animal is held and suddenly lowered to the ground the right leg is not extended like the other. There also seems a deficient power of grasping in the toes of the right foot. These pareses, although not extensive, were permanent. They were not accompanied by any perceptible deficiency in sensibility.

Whilst examining this Monkey on the fourth day after the operation, on taking hold of the right arm, a fit commenced, lasting for seven or eight minutes. It began with retraction of the right arm, followed by spasmodic flexion and extension at the elbow. This was succeeded by spasmodic flexion at the hip and slight extension at the knee. Still later, the head began to turn to the right, with clonic spasms, with twisting of the body to the right, and marked arching of the spine (concavity to the right).

The animal had a similar, but shorter, fit on the morning after the operation (seen only by the attendant). None others were observed.

The brain of this Monkey is shown in fig. 11, Plate 2.

The animal lived a year after the operation.

12.

Lesion.—Ablation of the left marginal gyrus (its posterior three-fourths) and the narrow adjoining strip of the external surface extending laterally as far as the [illegible]

[illegible]—Paralysis of right side of trunk and of right leg; partial paralysis of [illegible] seems to have a very imperfect power of extension from the [illegible]

[illegible] a few days after the operation by gangrenous cedema of [illegible] finally resulted in recovery, but not before the right [illegible] become lost. The animal was killed six months

13.

Lesion.—Removal of posterior two-thirds of left gyrus marginalis and a narrow adjoining strip of the external surface.

Result.—Paralysis of right leg. There also seems an inability to rotate the spine, but it is difficult to be sure of this. No other results were recorded.

This animal only lived one week, death being the result of enteritis, apparently brought on by chill (the room having been accidentally allowed to become cold). Except for the lesion, the brain was found to be perfectly healthy, without any sign of inflammation of surrounding portions.

The lesion is represented in fig. 13, Plate 2

14

Lesion.—Removal of the left gyrus marginalis.

Result —Paralysis of right leg and of trunk muscles on right side, so that the upper part of the body is turned round to the left. The right arm is at first partly paralysed, but by the third day this had become scarcely perceptible. For the first three days the right side of the body and the right limbs react less readily than the left to sensory, especially to tactile, impressions, but already on the fifth day this difference is no longer to be made out.

The animal died of enteritis three-and-a-half weeks after the operation.

The mesial surface of the left hemisphere is represented in fig. 14, Plate 2.

15.

Lesion 1.—Right marginal gyrus removed from just behind the sulcus of **Rolando** as far forwards as the anterior extremity of the precentral sulcus. The lower slope of the convolution posteriorly was, however, found at the autopsy to have been left.

Result.—Paralyses not very well marked. Slight paresis of left arm; when sitting, the animal props itself up by right arm, while left arm is kept flexed and adducted. It can, however, be freely used. When standing up, the weight of the body rests chiefly on the right leg, and in springing this leg is used almost exclusively. Extension of hip is deficient (? wanting) on left side. Left toes paresed; retain some power of grasping, but greatly weakened

Lesion 2.—Second operation, seven weeks after the first one. Ascending parietal, ascending frontal, and posterior part of first and second frontal gyri removed on same side as primary lesion. (This external part of the brain was found to be perfectly normal when exposed for operation, although in the previous operation all the veins passing from it into the superior longitudinal sinus had been tied. In most subsequent operations upon the marginal gyrus these veins were avoided and not tied.)

Result.—The immediate result of this operation was to produce *complete or absolute hemiplegia.* The right pupil was much dilated, the left contracted. The head and eyes were turned to the right, and the face was drawn over to the same side. After a few days, however, the hemiplegia appeared somewhat less complete. There was a very slight capacity to raise the left arm, and also ability to flex the left hip, when attempting to walk. The head and eyes can now also be moved to the left. Unfortunately the skin in this case sloughed, and the wound thus became partly open and septic, with the result that the animal died the fifteenth day after the operation. The effect of the failure to maintain the antiseptic character of the wound was also apparent in the extension of the lesion, the edges and bottom of which were softened and disorganised so as to render the post-mortem condition of the brain of less value than in other cases in which no such extension occurred We have, however, thought it worth while to reproduce the representations of it from both the outer and mesial aspects. It will be seen from these (figs. 15A, 15B, Plate 2) that the postero-parietal lobule is in part left, and also the posterior end of the marginal gyrus. The inferior border and the anterior end of the marginal gyrus also remain. Otherwise the whole of the motor areas upon the right side are destroyed.

16.

Lesion.—Removal at one operation of the marginal gyrus (its posterior three-fourths), ascending parietal, parietal lobule, ascending frontal and posterior half of transverse frontal convolutions on left side of brain. Lived seven days.

Result.—Absolute right hemiplegia, both limbs and trunk being paralysed. Head rotated to same side. Face drawn over to right. Trunk arched, with convexity to right. Right leg is dragged, right arm drops from shoulder. Can support itself only by aid of left limbs. Drinks with paralysed side of mouth immersed in the fluid. No recovery observed up to time of death, which occurred on the seventh day.

The brain is represented in fig. 16. It would appear as if part of the ascending parietal and the parietal lobule were not involved in the lesion, but in fact they were completely softened and undermined, so as to render it impossible to suppose that any part of them could have continued to perform its functions. The lesion of the marginal gyrus is very complete.

17.

Lesion.—Almost identical with that recorded of the preceding brain, but on the right side. The cortex of the whole frontal lobe, except the anterior fourth and a strip along the lower margin; the ascending parietal convolution. The lesion is more complete at the upper and lower ends of this than in the centre, where only the part next the furrow of ROLANDO appears to be involved; moreover it does not include the parietal lobule and the part of the marginal gyrus corresponding in longitudinal extent to the lesion upon the external surface.

Result.—Absolute hemiplegia, as in 16, but of course involving the opposite side of the body. The hemiplegia was absolute, although the parietal lobule and the upper two-thirds of the ascending parietal were not removed, at least intentionally. But there was a partial softening and undermining in these convolutions, probably produced by the interference with their vascular supply which was caused by the lesion, and sufficient to account for the fact that the paralysis extended to the parts with which the convolutions in question are connected.

This animal also lived one week only.

The superficial extent of the lesion is represented in fig 17, Plate 2.

18.

Lesion 1.—Excision of the posterior three-fourths of the left marginal gyrus. A small part of the lower edge of the convolution was, however, left, as the section of the brain shows (fig 18A)

Result.—Partial paralysis of right leg, especially the extensors of the hip and the flexors of the knee. No determinable paralysis of trunk

Lesion 2.—Second operation, twenty-one days later. In this operation most of the external motor areas were removed, including the anterior slope of the ascending parietal, the whole of the ascending frontal as far as the lower end of the fissure of ROLANDO, the posterior third of the superior frontal gyrus, and the part of the middle frontal gyrus included in the angle of the prefrontal sulcus. All this part of the brain was perfectly healthy when exposed for removal

Result.—There is paralysis with contracture of both right limbs, but the hemiplegia and prostration are not so complete as in the cases previously recorded, which is no doubt due to the fact that the lesion was not quite so extensive There is some slight ability to grasp with the fingers of the right hand, but none with the toes of the corresponding foot. There is distinct contracture at right elbow, hip, and knee; when actively climbing, the right arm and hand are occasionally employed, but not the corresponding leg No difference of sensibility can be determined upon the two sides. The knee-jerk is normal. (These notes were made two months after the second operation.) This Monkey was kept nearly four months after the second operation.

The brain is represented from above in fig. 18, and in frontal section in fig 18A. The section passes through the widest part of the lesion.

19.

Lesion.—Excision of both marginal convolutions (on the left side for the posterior three-fourths of the longitudinal extent, on the right side slightly less) The lesion, as shown by examination of the brain after death, does not quite reach either the upper or lower margin of the convolution, especially on the right side. It was followed by considerable shock.

Result.—Almost complete paralysis of trunk and leg muscles, but there is some ability to move, especially to flex, the legs, particularly the left leg When placed upon the floor, the animal seizes neighbouring objects and pulls itself up into sitting posture by arms; sits propped up on both arms with feet splayed out and knees in; appears unable to extend the spine or to move the tail, but head can be flexed, extended, and rotated.

The animal died on the ninth day.

The post-mortem elicited, as is frequently the case after these lesions, the existence of dysenteric ulceration of the solitary follicles of the large intestine The general surface of the brain was perfectly healthy, without any sign of clot or extravasation except just along the lesion.*

The hemispheres are shown, seen on their mesial aspect, with the full extent of the lesion displayed in figs. 19 R. and 19 L., Plate 2.

20.

Lesion.—Removal of posterior three-fourths of both marginal convolutions.

Result.—Complete paralysis of trunk and legs, except that the latter can be feebly drawn up under the abdomen. The Monkey assumes the attitude characteristic of this lesion (see p. 13 and fig. 20, Plate 3). Cannot sit up at all, but can drag itself about by its arms. No head or face paralysis.

Death on the eighth day, with symptoms of dysenteric diarrhœa.

The brain was sliced as a whole, so that no drawing of the superficial extent of the lesion was made, but the extent of the removal of the grey matter of the marginal convolutions is shown in section in the accompanying drawings (figs. 20A, B, C, and D), which are numbered successively from before back. It will be seen from these that it is only quite at the posterior end that any of the grey matter of these convolutions is left.

The animal itself is shown in fig. 20 (from a photograph).

21.

Lesion.—Removal of posterior three-fourths of both marginal gyri at one operation.

Result.—Paralysis of trunk and legs. The animal cannot sit up, but lies on one side, generally the right, with legs drawn up, and spine and tail stiffly flexed. This position of the trunk and limbs appears to be due to contracture of the muscles; it is most marked in the limbs of the left side. On the left side the foot is flexed, on the right it is extended; the toes are semiflexed on the right side, completely flexed on the left. When one attempts to straighten the legs or to move the tail pain seems to be caused. The arms and hands are not paralysed, and are used in progression as before described (pp. 13–14). Appetite good throughout.

Death from dysenteric diarrhœa on the twenty-seventh day. The solitary follicles of the large intestine were found after death to be extensively ulcerated.

On removing the brain a considerable clot, more or less organised, was found resting against the injured surface of the marginal convolution of the right side. Perhaps the irritation caused by this may have conduced to the strongly marked contracture of the muscles of the opposide side

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* Although we have only formally mentioned the healthy aspect of the rest of the brain in one or two instances, it is right that we should state once for all that in all the cases we have here recorded, unless the contrary is directly mentioned, all parts of the brain other than those destroyed in the operation presented on post-mortem examination a perfectly normal aspect.

The brain was sliced as a whole, and four sections through the lesion are represented in figs 21A, B, C, and D. These serve to illustrate the localisation and completeness of the removal.

22.

Lesion —Removal of both marginals in two operations.

Results —The first operation (on left side) produced the usual paralysis of the opposite hind-limb, which was dragged in progressing and hung down when the animal perched upon a bar All the other symptoms distinctive of this lesion are also observed (see p 14).

The second operation was performed on the eighth day after the first, the wound in the meantime having completely healed and the Monkey being perfectly well. The result of the second operation was to produce, as usual, paralysis of trunk and legs, except that the hips could be flexed and the knees extended (feebly on both sides, but more on the right side than on the left). The tail was rendered motionless. The body was propped upon and dragged forward by the fore-limbs. No deficiency in sensibility could be determined. Later, rigidity developed in both legs and in the tail, which was stiffly flexed over the spine. This Monkey was kept three months. Although its movements became much more active after some time than at first, this was due to the exercise of the unaffected muscles, there was no recovery in those in which paralysis had been produced by the operation.

The brain of this animal, which died in Long Vacation time, was injured on removing it from the skull, so that no drawings could be made to show the extent and depth of the lesion; but there is no doubt, from the notes made at the operations as well as from the symptoms, that it involved the posterior two-thirds of both marginal gyri, and was somewhat less complete on the left side than on the right.

23.*

Lesion —Excision of both gyri marginales† at one sitting.

Result.—The usual symptoms produced by this lesion, *i.e.*, complete paralysis of trunk and almost complete of legs, but with power to flex hips. Drags itself about by arms. Unable to sit up, but props itself up by aid of arms.

The animal lived four weeks after the operation.

The lesions are represented in figs. 23 R. and L., Plate 3.

24.

First Lesion.—The whole of the left occipital lobe was removed by an oblique incision along the parieto-occipital fissure. The piece removed included the extremity of the posterior cornu of the lateral ventricle, which was thus freely opened. No ill consequences resulted from this, however, and when on the 5th day the dressings were removed the wound was found to be completely healed.

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* Shown to the Neurological Society.

† That is, that portion of them shown to be excitable.

Result.—No muscular paresis. The animal seems to have some disturbance of visual consciousness of the images of objects which fall upon the left side of the retinæ, for an object, such as a raisin, presented to it on the right side of the visual line is either not noticed or its nature is not readily recognised. This condition, which was very well marked at first, gradually improved, until three months after the operation it could be no longer determined

Second lesion—Four months after the first operation the anterior half of the frontal lobe, including the orbital lobule, was removed upon the same side (the left) by a nearly vertical incision. The recovery was again rapid and complete.

Result.—The only noticeable symptoms which were produced by the second lesion were (1) some paresis in the opposite arm; and (2) an inability readily to turn the head to the opposite side.

Third lesion.—Ten weeks after the second operation the whole of the left temporo-sphenoidal lobe was cut away, with the exception of the hippocampal gyrus, which was, however, injured considerably. In this operation the descending cornu of the lateral ventricle was freely exposed, and the hippocampus major was excised in the greater part of its extent.

Result.—Immediately after the operation was completed there was some paralysis of the opposite limbs and defective sensibility on the opposite side of the body. But these results may well have been due to the temporary disturbance caused in the remainder of the hemisphere, by the loss of the support yielded by the temporo-sphenoidal lobe, and by the disturbance of the circulation in that half of the brain produced by the section and occlusion of many of its vessels. For, the next morning, on carefully testing for sensibility in various ways, no difference was determined upon the two sides of the body, and the paralysis of the limbs had disappeared, with the exception of the slight paresis of the upper limb, which had been left from the second operation. Vision for the images of objects falling upon the left half of the retinæ was again impaired, and this impairment lasted some time, but how long was not accurately determined. Experiments devised to test the consciousness of auditory sensations reaching the opposite ear gave no definite results.

The *permanent* result of these three ablations was, it will be seen, almost *nil*, although so much of the cortex of one hemisphere had been removed by them.

Fourth operation.—Of the remaining part of the cortex, which included the angular gyrus, the parietal lobule, the central gyri, parts of the transverse frontal gyri, the marginal gyrus, the gyrus fornicatus, and the hippocampal gyrus, all but the two last-mentioned gyri were removed three months after the third operation.

Result.—The result was the production of absolute hemiplegia with severe shock, from which the animal failed to recover, dying in the course of a few hours.

The brain is represented in figs. 24A and B, Plates 3 and 4, but the representations are mainly of interest as showing the completeness of removal of the frontal and occipital lobes, and the limits of the lesion upon the under-surface of the hemisphere.

25.

Lesion 1.—Left occipital lobe removed. The hemiopia (imperfect visual perception of objects on right of mesial plane) which resulted was accompanied by partial hemiplegia and œdema of the opposite foot (so that there was probably some hæmorrhage into the ventricle) The paralysis was, however, in great part gradually recovered from, but the hemiopia persisted, although in a diminished form, until three weeks after, when (*Lesion* 2) the right occipital lobe was removed. This was also followed by imperfect visual perception (of objects on left of mesial plane), but the animal was attacked by gangrenous cellulitis of the feet, and had to be killed sixteen days after the second lesion. In this interval of time there was little or no recovery from the visual imperfection.

The brain is represented in fig. 25. From this it will be seen that the removal of the occipital lobes has not been quite complete, especially upon the right side, not more than half of which has been excised.

26.

Lesions 1 *and* 2.—In this Monkey both occipital lobes (external and posterior surfaces and a part of the under-surface) were removed, with an interval of fourteen days between the two operations. A little of the external surface was, however, left intact.

Result.—The first lesion (on the right side) was followed by left hemiopia, which had not been recovered from when the second (on the left side) was established. The immediate result of the double lesion was to produce almost complete blindness This was gradually recovered from to a certain extent, so that, although small objects did not appear to be distinctly discerned, larger ones were seen and obstacles were avoided. There seemed after a time to remain a general impairmennt of visual perceptions, without, so far as could be made out, absolute blindness in any part of the field of vision, but of this we cannot speak with any certainty.

Lesion 3.—Two months after the removal of the left occipital lobe, and with the animal in the condition just described, the angular gyrus of the right side was cut away.

Result.—This operation was followed by complete hemiopia, the right side of both retinæ being perfectly blind. A threatened blow coming from the left side was not avoided, no objects appeared to be seen, nor was any food picked up if placed on the left side of the mesial plane of vision. This condition lasted without recovery until the animal's death (from dysentery) three months later.

The brain, viewed from behind and somewhat from above, is shown in fig 26

27.

Lesion 1.—Removal of the whole of the external and posterior surface of the left occipital lobe. The upper part of the angular gyrus was also to some extent involved in the lesion.

Result.—Right hemiopia apparently complete; objects on the right of the mesial plane are not seen. This condition lasted some weeks, but gradually improved, so that after five months the most careful testing failed to elicit any imperfection of visual perception.

Lesion 2.—Six months after the first operation the cortex of the quadrate lobule of the same side (the left) was removed. The result of this second operation, so far as could be determined, was entirely negative.

The brain is represented in figs. 27A and B, Plate 4.

28.

Lesion 1.—The greater part of the left temporo-sphenoidal lobe was cut away, the descending cornu of the ventricle opened, and the hippocampus major removed. The lesion included all but a small part of the hippocampal gyrus.

Result.—We could detect no difference of sensibility on the two sides, nor was there any other noticeable symptom either on the day after the operation or on any subsequent occasion.

Lesion 2.—A nearly equal extent of the right temporo-sphenoidal lobe was removed three weeks later, but on this side the gyrus hippocampi remained almost untouched. The ventricle was again opened and the hippocampus major cut away.

Result.—The result was again negative; again we could detect no deficiency in sensibility on the opposite side.

This animal contracted pneumonia and died on the fifth day after the second operation. The occurrence of this illness prevented any accurate testing of the other special senses.

The brain is represented in 6 figures on Plate 4, both right and left hemispheres being shown as seen (1) from without, (2) from below, and (3) in section.

29.

Lesion.—A large part of the left temporo-sphenoidal lobe was removed, the ventricle (descending cornu) opened, and a considerable piece of the hippocampus major excised. The superior temporo-sphenoidal gyrus, the anterior extremity of the lobe, and the hippocampal gyrus were only in part involved in the lesion.

Result.—We could detect no difference of sensibility upon the two sides. There was no muscular paralysis, nor any other obvious loss of function. We did not test this animal's hearing, intending to reserve the tests for this until the operation should be repeated upon the other side. This second operation was performed three weeks after the first (the wound caused by the first operation having completely healed, and the animal being to all appearance well on the third day), but was not followed by recovery, death being the result of shock

The left side of the brain of this Monkey is represented as seen from below in fig. 29, Plate 4.

30.

Lesion.—Ablation of right temporo-sphenoidal lobe and hippocampus major.

The lesion involves only the middle of the hippocampal gyrus.

Result.—As regards sensibility, we could detect no difference on the two sides. As regards hearing, when the ear on the same side as the lesion is stopped the animal seems unable to hear slight sounds.

No other result was obtained. The animal was kept seven weeks.

The lesion is shown in fig. 30A (Plate 5) as seen from the outer aspect, and the extent to which the hippocampal gyrus is involved is exhibited in fig. 30B.

31.

Lesion—In this animal the greater part of both temporo-sphenoidal lobes was removed in four successive operations, with an interval of rather more than a month between the first and second, about twelve days between the second and third, and a little more than a month between the third and fourth. The first two operations involved all but the superior gyri, but the hippocampal convolution was not reached by the lesion except at its middle part on the right side, where at one point only the injury extended quite to the edge of the hemisphere. Upon the left side the apex of the lobe was left intact, but on the right side it was almost entirely destroyed. In the third operation both the superior temporo-sphenoidal gyri were cut away; but on the right side the superior extremity of the gyrus for about three-eighths of an inch also remained intact, and on the left side the lower extremity. In the fourth operation the hippocampus on the right side, which had not been reached at the first operation, was exposed and excised along a considerable extent

Result.—The extensive lesions in the brain of this Monkey produced no discoverable symptoms, with the exception of a temporary diminution of sensibility, lasting about a week, or rather more, upon the left side, following the operation for removal of the right hippocampus major. There was no motor paralysis, no diminution of sensibility, even for tactile impressions, and hearing was to all appearance quite acute even the day after the destruction of both temporo-sphenoidal gyri (the remainder of the temporo-sphenoidal lobes having, as we have seen, been previously removed).

This animal was kept alive for nearly five months after the first operation.

The brain is represented in figs. 31A, B, C, and D.

32.

Lesion—Ablation of the greater part of the right temporo-sphenoidal lobe (a small (postero-superior) part only of the superior gyrus, the posterior extremity of the second gyrus, the tip of the lobe anteriorly and the posterior part of the hippocampal gyrus being left intact). The hippocampus major was removed in the greater part of its length.

Result.—We could not detect any deficiency of cutaneous sensibility on the left side of the body, nor was any defect of vision perceptible. As regards the other special senses, we were unable to arrive at any satisfactory result. The animal was kept under observation seven weeks after the operation.

The brain is represented as seen from below and the right side in fig. 32A, and in section in fig. 32B.

33.

Lesion.—Complete removal of the left temporo-sphenoidal lobe, including the hippocampus major. The lesion also involved the under-surface of the occipital lobe.

Result.—This Monkey survived the operation only two days, so that the results are very imperfect, and, owing to the collapsed condition of the animal during that time, observations upon the special senses could not be properly conducted. It was, however, clearly ascertained that marked diminution, if not complete loss, of tactile sensibility was produced upon the opposite side of the body, together with diminished sensibility to painful impressions.

The condition of the brain is illustrated by figs. 33A, B, and C (Plate 5).

34.

Lesion.—Removal on the right side of the whole of the lower part of the temporo-sphenoidal and part of the lower surface of the occipital lobe. The hippocampus major and minor were also excised. The superior temporo-sphenoidal gyrus was left, as well as the postero-superior part of the second gyrus. After death it was found that there had occurred softening and destruction of the whole of the lower surface of the occipital lobe, and a patch of softening also extended round the posterior extremity of the hemisphere to the upper surface of this lobe, reaching along the mesial edge nearly to the parieto-occipital fissure (fig. 34B).

Result.—Next day there was no response to tactile impressions applied to the left side of the body and left limbs, and lessened response to painful impressions was also observed, although both produced a ready response when applied to the right side. The day after, the response to painful impressions was somewhat quicker, but tactile impressions still produced no reaction on the left side. The defective sensibility of the left side was found, however, to undergo gradual improvement from day to day; but even three-and-a-half months after the lesion there was still a difference of sensibility upon the two sides, that of the left side being distinctly lessened.

Hemiopia was also produced by the lesion, or by the subsequent changes. This was of such a character that the right side of both retinæ was blind, *i.e.*, no objects were seen which were on the left side of the mesial plane of vision. This hemiopia was permanent; lasting, that is to say, until the animal was killed three-and-a-half months after the operation.

Experiments upon the other special senses, as is usually the case with unilateral lesions, gave no definite results.

There was no muscular paralysis.

The brain is represented as seen from below (right hemisphere) in fig 34A (Plate 6), and in section in figs. 34C, D, E. The posterior aspect of the right hemisphere is given in fig. 34B.

35.

Lesion 1—Removal of a large part of the left temporo-sphenoidal lobe, with the exception of the superior gyrus The hippocampus major was included in the removal, but the gyrus hippocampi only partially (see fig. 35B, Plate 6)

Result—No difference could be detected on the two sides as regarded sensibility. Hearing was not tested.

Lesion 2.—One month later the gyrus fornicatus and the quadrate lobule of the same side were removed as completely as was possible.

Result.—In testing the next day, it is found that there is complete insensibility to tactile impressions over the whole of the right side, although on the left side these produce a marked reaction. Even to a prick, hard pressure, or the contact of a hot wire, there is only a slow reaction on the right side. The animal was completely recovered from the operation by the third day, but retained the same condition, the right side becoming every day, however, somewhat more sensitive to impressions. But this recovery proceeded only to a certain extent. Even three-and-a-half months after the second operation (when the animal was killed) there was still a distinct difference in sensibility on the two sides of the body.

No hemiopia was noticed in this Monkey, nor could any definite results be arrived at regarding the other special senses

The lesions are shown in figs. 35A, B, and C.

36.

Lesion.—Removal of a considerable part of the left gyrus fornicatus. During the operation there was much venous hæmorrhage, and several of the veins passing from the outer surface into the longitudinal sinus had to be tied. The marginal gyrus and the motor region of the outer surface of the hemisphere were also somewhat compressed in the endeavour more completely to expose the gyrus fornicatus, and, as the post-mortem examination of the brain showed, they did not escape permanent injury, especially the gyrus marginalis (see fig 36, Plate 6).

Result.—On testing for sensibility the next day, "it is found that the right upper limb, and the whole of the right side of the body as far as the level of the iliac crest, is almost completely insensible to touch, to the prick of a pin, and to a jet of cold water suddenly applied. A heated wire is felt when applied to the back of the fore-arm, but produces no reaction elsewhere upon the right arm and hand unless heated to excess. The ear and the right side of the head are apparently as sensitive as on the left side, but the right leg, although by no means anæsthetic, is distinctly less sensitive than the left. The leg, trunk, and arm muscles appear weakened, although the right limbs are still freely used. The animal is to all appearance quite well and lively.

"Two days later (on the third day) the condition as regards sensibility is exactly the same, but the pareses, especially of the leg, are less marked.

"During the rest of the week following the operation the symptoms are much the same, but the right side seems to be slowly recovering. It requires, however, a considerable stimulus to produce any response, and the interval between the stimulus and the response is much lengthened; the reaction, when it does appear, being often of the nature of a sudden start. There is also some failure to localise the seat of irritation, and the left limb is often scratched by the animal each time that the right limb is irritated (condition of *allochiria*). The right arm and leg are still paresed."

The animal was kept for seven weeks, at the end of which time the difference of sensibility was still apparent upon the two sides, both for tactile and painful sensibility (prick, heat, induction shocks), although it had distinctly diminished.

An attempt was then made to remove the gyrus fornicatus of the other side, but the animal succumbed to the shock of the second operation.

The left hemisphere is represented on its mesial aspect in fig. 36. From the superficial view, the lesion of the gyrus fornicatus appears less extensive than is actually the case, for sections showed that this convolution, although imperfectly removed, was undermined by the incision that was made along it preparatory to its ablation.

37.*

Lesion 1.—The anterior part of the left gyrus fornicatus was removed from about the level of Y forwards.

Result.—The external ear of the opposite side gives no reaction either to tactile impressions or to impressions producing pain elsewhere (prick, heat, electric shocks). It could not be determined whether any other parts were as completely insensible.

Lesion 2.—One week later the greater part of the remainder of the convolution was cut away.

Result.—"There is great diminution of sensibility over the whole of the right side. Tactile impressions are not perceived, or at least produced no reaction; painful impressions, such as a prick or a burn, are only slowly perceived and are then not localised. To every such stimulus, no matter to what part of the right side it is applied, the animal responds in the same manner, viz., by scratching the right fore-arm." This phenomenon (a form of *allochiria*) was exhibited for about a week after the second operation; it then disappeared.

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* This animal was exhibited to the Physiological Society.

"Tested on the tenth day after the operation, there is no reaction produced on pricking any part of the right arm, and only a very slow reaction on applying a similar stimulus to the right side of the trunk and to the right ear The leg reacts more readily, but is distinctly less sensitive than the left leg."

After this time the condition as regards sensibility began slowly to improve, especially in parts. "Reaction is now obtained on stimulating the right hand and arm below the elbow, but none from the upper arm, and very little from the upper part of the trunk down to the level of the iliac crest The right ear is still quite insensitive, but the side of the face is sensitive. The right foot is rather more sensitive than before, and indeed the whole lower limb reacts, although more slowly and less markedly than on the left side, both to tactile and painful impressions."

Three months after the second operation the whole of the right side still showed a great diminution of sensibility as compared with the left. The difference was least marked in the arm at and below the elbow. The animal was then killed and the brain examined.

It appears that the lesion involves the greater part of the gyrus fornicatus and the anterior portion of the quadrate lobule, but for a small extent, about 5 mm in length, near the anterior end of the corpus callosum the convolution is almost intact. The gyrus marginalis is injured at two places, viz., to a small extent posteriorly, and also anteriorly in the prefrontal region. Close to the latter lesion there is a small patch of softening on the external surface.*

The mesial surface of the left hemisphere is shown in fig. 37A (Plate 6), and four sections through the same hemisphere in figs. 37B, C, D, and E The sections are taken at about the situation of the lines which are lettered correspondingly in fig. 37A.

38.†

Lesion.—The posterior part of the left hippocampal gyrus was scooped away, the occipital lobe being raised from behind and the scoop introduced beneath it. The result of this *modus operandi*, as shown on post-mortem examination, was to cause extensive softening of the occipital lobe. Whether from this destructive process going on in the brain, or from some other unknown cause, the animal did not survive the operation more than seven days. During the whole of this interval there was considerable diminution of sensibility upon the right side as compared with the left, without any sign of motor paralysis.

The superficial extent of the lesion is shown in fig. 38A, Plate 6, and the deep extent in the sections in figs. 38B, C, D, and E.

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* There was no perceptible paresis produced by the operation in this Monkey. The right hand was used much less than the left, but many Monkeys are left-handed, and we had not previously determined whether this was such an one. Even had it not been so, the diminished use of the right hand might well have been produced by the loss of tactile sensibility of that limb.

† This animal was exhibited to the Physiological Society.

39.

Lesion 1.—Partial removal of the left gyrus fornicatus. A sharp scoop was carried along the convolution with the intention of removing the grey matter as completely as possible; but the post-mortem examination of the brain showed that, as is so often the case in these cerebral ablations, the amount removed was far less than was anticipated. At two places only was there much destructive lesion of the convolution, viz., in front near the anterior extremity of the corpus callosum, and behind near the quadrate lobule. The remainder of the gyrus between these points is almost intact, except along its upper margin, near the calloso-marginal sulcus. The instrument must have been carried along the line of this sulcus, for the lower border of the gyrus marginalis is destroyed to a corresponding extent.

Result.—The next day the animal does not react to tactile impressions applied to the right side of the trunk as far down as the flank, and also all over the right arm, and hardly reacts to a prick or jet of water on those parts, but the head and the hind-limb of the right side seem fairly sensitive. There is some muscular paresis of the whole right side.

The loss of sensibility upon the right side was maintained, but in a gradually lessening degree, during seven weeks, when a further operation was performed, viz.:—

Lesion 2.—Removal of the posterior part of the limbic lobe as it bends round the splenium of the corpus callosum.

Result.—" It is doubtful if there is any difference produced by this second lesion. It is still the right arm and right side of the trunk which show diminished sensibility."

Lesion 3.—Two weeks after the second operation the skull was removed over the left occipital region, the occipital lobe raised, and the posterior part of the hippocampal convolution scooped away from behind.

Result.—Our impression is that the anæsthetic condition of the right side of the body was better marked as the result of this third ablation, although we cannot positively affirm this. We will content ourselves with giving the results of a careful mapping out of the anæsthetic region which was made a fortnight after the third operation. So far as we could determine, the symptoms then recorded persisted without perceptible change until the animal was killed three months later. The testing was performed mainly by gentle and repeated prickings with a small pin, but the difference upon the two sides was also tested by induction shocks.

" On the right side of the head, neck, and trunk no reaction is obtained until the flank is reached, when there is immediate manifestation of sensibility. The right leg reacts at once to a prick, but not to gentle scratching with the pin point, sufficient to produce marked reaction upon the left side. Of the right arm the elbow and palm of the hand react readily, the back of the fore-arm hardly at all, the back of the upper arm only slightly. Reaction is also obtained by stimulating in the axillary and pectoral regions.

" There is distinct muscular paresis of both right limbs, but more of the arm than

"There is hemiopia; objects on the right side of the mesial plane not being seen." This is accounted for by the fact that the interference with the occipital lobe which occurred in the two later operations produced, as the post mortem examination showed, extensive softening of that portion of the brain.

The superficial extent of the lesions is represented in fig. 39.

40.

Lesion.—A cut was made along the anterior two-thirds of the right gyrus fornicatus, and the grey matter of the convolution was completely scooped away. The post-mortem examination showed that the marginal gyrus was also slightly injured, especially in the prefrontal region, and there were some small patches of softening on the external surface which had probably been caused by the drawing aside of the brain in endeavouring the better to reach the gyrus fornicatus.

Result.—There was at first some paresis of the limbs and of the facial muscles on the left side. For ten days or more no reaction whatever was obtained either by tactile or painful impressions (pricks) applied to the left side, although the reaction was marked on the right side. "Even a hot wire causes very slow reaction, and the impression is apparently not localised." After this time there was some return of sensibility so far as painful impressions were concerned, the improvement being most marked at the back of the fore-arm.

A month after the operation "reaction to painful impressions is manifested over the whole of the left side, but much less markedly than on the right side; but there is still no reaction to tactile impressions applied to the left side After a time, however, tactile impressions begin to produce reaction upon the left side also, but they are responded to far less markedly than on the right side." This was still the case ten weeks after the operation, when a second lesion, viz., the removal of the left gyrus fornicatus, was attempted, but proved fatal.

The lesion in the right hemisphere is shown superficially in fig. 40A, Plate 7, and in section in fig. 40B.

41.

Lesion 1.—Destruction of the middle and posterior part of the right hippocampal gyrus from behind by raising the occipital lobe.

Result.—The immediate result produced by this operation was to cause almost complete loss of reaction to tactile impressions in the left limbs and on the left side of the trunk, and greatly diminished reaction to painful impressions. The left ear and the left side of the head and face did not participate in this condition, which persisted for a few days, becoming gradually less marked, so that ten days after the operation the difference of reaction upon the two sides of the body was only slight.

Seven weeks after the establishment of the first lesion, by which time no difference of sensibility could any longer be detected upon the two sides, a second operation was performed upon the same animal. This consisted (*Lesion* 2) in the attempted destruction of the gyrus fornicatus upon the same side as the hippocampal lesion, but the post-mortem examination showed that the destruction of that convolution was not complete. Only about the middle third of the gyrus fornicatus was involved in the lesion, and even here at places the part next the corpus callosum remained undestroyed. On the other hand, an equal extent of the marginal gyrus along the calloso-marginal sulcus was injured.

Result.—This second lesion again produced a very considerable deficiency of reaction to tactile impressions and a certain amount of deficiency of reaction to painful impressions over the whole of the left side of the body. There was also some paresis of the left leg. This condition persisted until the death of the animal ten days after the second operation.

The lesions are shown in figs. 41A to D.

42.*

Lesion 1.—Removal of the anterior two-thirds of the left gyrus fornicatus.

Result.—The immediate result was the production of a great diminution of sensibility over the whole of the right side of the body. The insensibility was for the first two or three days complete, even to pricking and a hot wire, on the right side of the trunk and in the right upper limb. A slight reaction is obtained on pricking the root of the tail on the right side, and more on applying the same stimulus to the right leg. There was also at first some muscular paresis on the right side, especially of the leg.

A week after the operation the condition was much improved.

There is now reaction over the whole of the right side to painful impressions, but often want of localisation of the seat of these impressions, a totally different part being scratched from that which is stimulated.† The muscular paresis is now scarcely, if at all, apparent.

Recovery proceeded gradually, so that after a time the difference of sensibility of the two sides is hardly perceptible, except about the arm and shoulder and in the foot.

Lesion 2.—Eleven weeks after the first operation, this last condition being still maintained, the right gyrus fornicatus was exposed, and injured by scratching its surface with a needle. This, however, produced no perceptible result, and after a fortnight the animal was killed and the brain examined, when it appeared that the permanent injury caused by the needle operation was so slight as to be almost imperceptible.

The lesion of the left hemisphere is shown in fig. 42, Plate 7.

43.

Lesion.—The posterior part of the left hippocampal gyrus was destroyed from behind by raising the occipital lobe.

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* Exhibited to the Physiological Society.

† Compare Nos. 36 and 37.

Result—The immediate result produced was great diminution of reaction both to tactile and painful impressions over the posterior part of the right side of the body, with slight diminution over the whole side, the reaction being slower than on the left side.

This animal was accidentally strangled by its cord on the fifth day, so that the further progress of the symptoms could not be followed.

The lesion is represented in fig. 43.

The expenses of this investigation have been chiefly defrayed by aid of a grant from the Association for the Advancement of Medicine by Research

II. *On the Organisation of the Fossil Plants of the Coal-Measures.*—Part XIV. *The true Fructification of* Calamites.

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[Plates 8–11.]

The systematic affinities of the Carboniferous *Calamites* have now been a moot question for close upon fifty years—the period that has elapsed since 1828, when, in his 'Prodrome d'une Histoire des Végétaux Fossiles,' Adolphe Brongniart first suggested their relationships to the recent Equisetums. At this time nothing was known of examples of *Calamites* encased in a thick vascular cylinder; a product of the exogenous mode of growth resulting from the action of a cambial ring. At a later period Brongniart obtained such examples from Autun and elsewhere. But having then a conviction that no Cryptogamic stem could undergo an exogenous development, he concluded that two classes of plants had been comprehended in the genus *Calamites;* the one Equisetiform, to which he continued to give the old name, the other a Gymnospermous type, to which he assigned the name of *Calamodendron.* His well-merited influence led to a wide-spread acceptance of these views; but their correctness began to be seriously questioned many years ago, on morphological grounds.

After a prolonged conflict the conclusions of those who insisted upon the Cryptogamic character alike of *Calamites* and of *Calamodendron* have met with an extensive, though not universal, acceptance. Meanwhile both the opposing schools of Palæontologists recognise the importance of discovering the fructification of these plants. Mr. Carruthers believed that he had found it in examples of *Calamostachys Binneyana,** and Mr. Binney arrived at a similar conclusion.† I have always rejected these conclusions, because of the conspicuous differences between the morphology of the Calamitean twig and that of the axis of the *Calamostachys.* These differences appeared to me much too great to make it possible for the one ever to have been a prolongation of the other.

In 1869 I published in the 'Memoirs of the Literary and Philosophical Society of

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* 'Journal of Botany,' December, 1867.

† 'Palæontographical Society,' volume for 1867.

Manchester'[*] a memoir "On a new form of Calamitean Strobilus from the Lancashire Coal-measures." The specimen described was found by Mr. BUTTERWORTH in a nodule from the Upper-foot coal in Strinesdale, near Saddleworth, in Lancashire. It was but a fragment, consisting of three nodes and two intermediate internodes Its basal and terminal nodes were alike wanting. The portion in our possession belonged rather to the lower than the upper part of the strobilus. Though but a fragment, its well-preserved internal organisation sufficed to show the general features of the strobilus, which differed widely from those of any Carboniferous fructification previously observed.

I ventured to construct a restored diagram of this strobilus,[†] and also pointed out a peculiar arched arrangement of the vessels of the xylem at each node, which I had hitherto seen only in the true *Calamites.* This fact, combined with other structural peculiarities equally Calamitean, led me to conclude that the strobilus was not only the fruit of a highly developed form of *Calamites,* but that it was the only one hitherto discovered which had any claim to that position.[‡]

Seventeen years elapsed before further traces of this fruit were discovered. But a few weeks ago Mr. JAMES LOMAX, of Ratcliffe, one of that small band of auxiliaries to whose diligence as collectors I have long been indebted for many of the materials upon which my researches have been carried on, brought me some new sections made from a nodule given to him by another of my assistants, ISAAC EARNSHAW, of Oldham. To my delight I found in these sections several specimens of the long-wished-for strobilus. What remained of the nodule was subsequently cut in such directions as promised to afford the best results. We have now not only much additional knowledge respecting the structure of the strobilus, but the clearest proofs that I was not mistaken in 1869 when I expressed my strong conviction that it was the true fruit of *Calamites.* The most absolute of these proofs is seen in the fact that each of three of these newly-discovered strobili had its basal peduncle attached to it ; and that these peduncles are ordinary Calamitean twigs of the type to which our French friends have long assigned the generic name of *Arthropitus,* and which they have, until recently, regarded as a Gymnospermous genus.

The sections represented in the plates have been made in as many directions as our specimens admitted of; the only way in which their complicated structures could be resolved.

Like the *Calamites,* each strobilus has a fistular medulla. The fistular cavity, marked *a* in each figure displaying it, is surrounded by a thin medulla, *b.* In the transverse sections, figs 1, 2, 3, and 4, (Plates 8, 9), this tissue resembles a very regular parenchyma, the cells of which are largest near the periphery of the fistular cavity. In the longitudinal sections they are seen to be very variable in size and form. This variability is well seen in fig 6, *b*, where nearly every cell is accurately delineated, and in fig 5 their general character is represented as correctly as the size of the figure admitted of. Many of these cells have rectangular transverse septa, in others these septa are oblique and overlapping. The latter form especially prevails in fig. 5. These medullary cells are usually most elongated vertically in the internodes, becoming much shorter, and their arrangement much less linear, at each node.

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[*] Third series, vol. 4.

[†] *Loc. cit.*, Plate 8, fig. 13.

[‡] See also the First Edition of BENNETT and VINES' translation of SACHS' 'Text Book of Botany,' p 377, where, by some oversight, the strobilus is referred to under the name of *Volkmannia Dawsoni,* which is a very different plant The error was corrected on p 408 of the Second Edition of the same work.

The peripheral limit of this medulla may be regarded as marked, in transverse sections, by a circle of longitudinal canals, which are constant as to number throughout the entire length of the axis of each individual strobilus In one example their number is 16; in each of four others it is 18; and in a sixth it is 20. These canals are unquestionably identical with the internodal canals of the ordinary *Calamites*, from which, as seen in the peduncles of the strobili they present no differences whatever; but within the strobili themselves, especially at the nodes, we find these canals arranged in pairs, as seen at *c*, *c*, in figs. 1, 2, and 4. This apparent dual arrangement is produced by a peculiar segmentation of the axis at and near each node, yet to be described. The canals have a mean diameter of about $\frac{1}{400}$ ($\cdot$0025) of an inch, one of them is seen at *c* in the long radial section, fig 6 (Plate 11); and they also appear more interruptedly at the points *c*, *c*, of fig. 5 (Plate 10).

The tissues which closely invest these canals are dense and their elements minute; they consist, on the medullary side, of small cells; but transverse sections reveal, on the cortical side of each canal, a wedge-shaped bundle of small vessels or tracheids, fig 2, *d* Each wedge is composed of several longitudinal vascular laminæ, which, starting from a canal, diverge somewhat as they proceed outwards, thus giving to each bundle the wedge-shaped contour seen in transverse sections of young *Calamites*. The larger medullary cells, already referred to, extend outwards between each pair of the canals and their vascular bundles (fig. 4, *b'*); these cells represent the primary medullary rays of the ordinary *Calamites*.

In Plate 11, fig. 6, *d*, some of the vessels of one of these wedges are seen outside the canal, *c*. Their number increases at *d'* as they approach the node, *f*, where the continuity of the individual vessels is interrupted; a result either due to a disturbance of their parallelism, or, what is also probable, some of them may resolve themselves into shorter tracheids. Whichever may be the case, these vessels or tracheids arch over the node, as they have long been observed to do in the *Calamites*. This arrangement is due to the circumstance that the first-formed of these vessels or tracheids were very short, not extending beyond each node into the adjoining internodes; the additions made exogenously to the exterior of those previously formed became successively more and more elongated; hence they described a series of arches, each arch enclosing the smaller one upon which it rested, whilst its two extremities encroached increasingly upon the internodes, *d''* and *d''*, above and below the node. This arrangement, which first suggested to me the idea that these strobili must be Calamitean, is also seen in Plate 10, fig 5, *d'*, *d'*. At the several points, *b'*, *b'*, of the latter figure these vessels are wanting, the section having passed, at these points, between two vascular wedges, *i e*, in the radial planes of primary medullary rays.*

The vessels composing these bundles are small, their mean diameter being less than $\frac{1}{800}$ (.00125) of an inch. Their structure is not well preserved in these strobili, but enough remains to show that, whilst some of them are reticulated (Plate 8, fig. 7), others are barred (fig. 8); amongst the latter we find some of the type so characteristic of the *Calamites*, in which the fissures, representing the bordered pits of the common scalariform vessel, are so enlarged vertically as to assume an oval form (Plate 9, fig 9).

The Cortex.—At each internode this is an extremely thin cellular layer outside the ring of vascular wedges; but where the broad primary medullary rays separate those wedges there is no distinct line of separation between the cells of the cortex and those of the medulla (Plate 10, fig 5, *b'*, *b'*). At each node the cortex expands into a cellular lenticular disk. This is an organ of considerable thickness at its centre, but becomes rapidly thinner peripherally. At its outer margin it subdivides into a number of free bracts, which curve upwards, investing the sporangia occupying each internode, whilst their tips rest upon the bases of the bracts of the next superior nodal disk (Plate 10, fig. 10, *k*, *k*). The greater portion of the thick central part of this disk lies, as is shown in Plate 10, fig 5, *h*, *h'*, *h''*, and Plate 11, fig. 6, *h*, *h'*, not on the plane of the node, but a little above it, whilst its gradually contracted vertical extensions in opposite directions invest a considerable portion of each internode above and below the central plane of the disk. In its thicker portions this organ is composed of a mass of coarse parenchymatous cells, intermingled with prosenchymatous ones (Plate 10, fig. 10, *h*, *h'*, *h''*, fig. 5, *h*, *h'*, and *h''*, and Plate 11, fig. 6, *h*). As it extends outwards from the central axis of the strobilus, this disk first bends downwards, but soon returns upwards with a bold curve, where its bracts, as already stated, enclose the entire internode. Its thinner peripheral portions are chiefly composed of prosenchymatous cells (Plate 11, fig. 6, *h'*).

A verticil of long slender sporangiophores springs from the upper surface of this disk, free, though not far, from the central axis of the strobilus. The base of one of these is seen at fig. 5, *l*, and a similar one at fig. 10, *l*; whilst at *l'* of the latter figure the entire length of one of these organs is preserved. In my memoir of 1868 I attempted a restoration (*loc. cit.*, fig. 13) of this strobilus, in which the only feature of importance requiring correction is the direction given to this sporangiophore. Having then only discovered its basal portion (*loc. cit*, fig. 6), I made it ascend into the internodal area too perpendicularly, instead of bending its ascending portion obliquely outwards as well as upwards

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* In describing these xylem structures, I have employed the alternative expressions, vessels or tracheids, because, in these fossil plants, it is absolutely impossible to determine with which of these elements we are dealing.

The above illustrations of vertical sections of these strobili render an understanding of the transverse and oblique ones easy Plate 11, fig. 11, is a transverse section, enlarged 36 diameters, of a peduncle of a strobilus. In one of my specimens this peduncle was sufficiently long to furnish four such sections All the specimens I have seen have exactly the same structure, only varying slightly in the number of the vascular wedges and internodal canals We have a fistular medullary cavity at *a*, which is constricted, but not subdivided by diaphragms at the several nodes, the medullary cells invest this cavity at *b*. A verticil of internodal canals is seen at *c*, each canal having in close contact with its outer side the vascular wedge, *d* Intermediate between each two canals and their associated wedges we have the primary medullary rays, *b′*. Each of these features is absolutely identical with what we find in a young Calamite of the Arthropitan type The diameters of these peduncles range between $\frac{1}{9}$ (11) and rather more than $\frac{1}{12}$ (·16) of an inch. As is so commonly the case with ordinary Calamites, every one of them is decorticated. Plate 8, fig 4, represents a transverse section made in a plane a little below that of the greatest diameter of a nodal disk. Its medullary cavity, *a*, medullary parenchyma, *b*, and internodal canals, *c*, do not differ materially from the same structures as seen in the sections of the peduncle, but externally to these structures we now discover an enlarged cortical zone, *e*, in which we find nine large vertical lacunæ, *i*, each having an oval section. These lacunæ can scarcely fail to remind us of those which occupy a similar position in the cortex of the living Equisetum The two differ in one respect. In the living plant we have one such cortical lacuna between each two of the internodal canals (the *carinal* canals of SACHS) But in the fossil strobilus we find one cortical lacuna between every alternate *pair* of internodal canals. Plate 8, fig 2, represents a transverse section through the sporange-bearing portion of a strobilus, made near the middle of an internode, at which point the intersected axis, *a*, *b*, *c*, *d*, differs but little from the corresponding transverse section of the peduncle, fig. 11. But it is otherwise with figs. 1 and 3, each of which represents a section of which one-half passes through a nodal disk at a higher level than was done in the specimen fig. 4. At *h*, *h*, in each of the figures 1 and 3, where the disk extends peripherally beyond the lacunæ, *i*, it consists of the coarse parenchyma shown in fig. 5, *h*, *h′*, and *h″*, and in fig. 6, *h*.

In the specimen, fig 1, the section has been made obliquely through the strobilus, having passed through the nodal disk at its lower half, but ascended into the internode above the disk at its upper margin; here we see the cortical lacunæ at *i*, *i*, whilst at *i′*, *i′*, they are only represented by mere concave longitudinal grooves on the exterior of the axis, which grooves become less and less conspicuous as we approach the centre of the internode, as is shown in Plate 8, fig. 2. On each side of the segment, *h″*, of the disk we discover two small cuticular lacunæ, *i″*, *i″*, which we shall meet with again in figs. 17 and 18. At the outer angle of each of these small lacunæ we find a sporangiophore, *l′*, intersected transversely close to where it sprang from the nodal disk. These sporangiophores, along with similar ones near to them, are part of a verticil of twenty, the remaining sixteen of which are seen to recede further and further from the central axis of the section until, at *l*, *l*, they become isolated amongst the spores of the internode above the disk from which they spring

The number of these sporangiophores is invariably identical with that of the internodal canals, *c*, and of the vascular wedges external to those canals. It is also exactly double that of the *larger* cortical lacunæ, *i*, of the nodal disk. Transverse sections of these sporangiophores vary somewhat in form, but such sections always approximate to the contour of fig 12, Plate 10. Apparently they consist only of prosenchymatous cells, disposed longitudinally; but it is scarcely probable that they should not contain a small vascular bundle of some kind. I have, as yet, discovered no trace of any such bundle, either given off by any of the axial vascular wedges, or traversing any one of my numerous sections of the cellular nodal disk.

The Sporangia.—Combining sections made in various directions, as in figs 2, 3, 13, and 14, I have been enabled to determine the arrangement of these organs. Fig. 2 we have already seen to be a transverse section across an internode. This strobilus seems to have been compressed laterally. The sporangia have been arranged in two concentric verticils, *m* and *m′*, between which the sporangiophores passed obliquely upwards and outwards.

Plate 9, fig. 3, is an oblique transverse section which has passed through the descending portion of a nodal disk, intersecting the bases, *k*, of the peripheral bracts at the upper part of the figure; hence it has failed to intersect any of the sporangia. But on its lower half it has almost cut through the strobilus in the plane of the obliquely ascending sporangiophores At this latter part we again discover the two series of sporangia, *m* and *m′*, and the sporangiophores at *l*, *l*.

Plate 11, fig. 14, represents a yet more oblique section, which passed through two nodal disks, *h* and *h′*, and three internodes, *g*, *g′*, and *g″*. Both *g* and *g′* show the two verticils of sporangia at *m* and *m*.

Plate 9, fig. 13, represents the only fragment of a true tangential section I have been able to obtain, and this is but an imperfect one, owing to a circumstance yet to be described. In this section the marginal bracts of two nodal disks are intersected at *k*, *k′*, and the two verticils of sporangiophores ascending from these disks are seen at *l*, *l′*. The walls of the sporangia constituting the upper and inner verticil of the internode *l′* are present at *m′*, and the sporangiophores at *l*, *l*.

Several points are demonstrated by the facts just described: the sporangia are very numerous; they are all arranged radially in two verticils; as is shown by fig. 13, *m′*, their vertical length much exceeds their transverse diameters; their perpendicular lateral surfaces are flat and virtually parallel to each other, allowance being made for the fact that, seen in transverse sections, the inner border of each sporangium is somewhat thinner than its outer one. In the inner verticil this inner border has a mean diameter of from $\frac{1}{150}$ (·0066) to $\frac{1}{50}$ (·02) of an inch, whilst their peripheral margins in the same verticil range between $\frac{1}{80}$ (·012) and $\frac{1}{50}$ (·02) of an inch. In the outer verticil the tangential diameter of each sporangium is rather greater—ranging from $\frac{1}{50}$ (·02) at their inner edges to $\frac{1}{30}$ (·033) of an inch at their peripheral ones. I have sought in vain for evidence showing where and how these sporangia are attached to the sporangiophores. As a rule, each sporangiophore appears to be the point at which four sporangia, two from each verticil, meet, as is the case with the genus *Calamostachys;* but there seem to be exceptions even to this arrangement, apparently due to the number of the sporangia being less constant than that of the sporangiophores. The wall of the sporangium is composed of a single layer of cells (Plate 10, fig. 15, *n*) flattened externally, but projecting convexly into the interior of the sporangium. The cell-walls, especially the inner and lateral ones, are slightly thickened. Each spherical spore (fig. 15, *o*) is enclosed within a ruptured mother-cell, *o′*, and has a small dark mass in its centre, the nature of which is doubtful.

In several of my sections, especially fig. 1, the sporangia are in a noteworthy condition; whilst some of the sporangia retain their sporangial walls, these walls have wholly disappeared from others. Thus in the section, fig. 1, the only traces of them which remain are a few isolated fragments. The same is the case at *m*, in the lower part of the internode *g* of fig. 13. Other sections show smaller portions of sporangia in a similar state. In such examples the sporangiophores are simply surrounded by compact masses of free spores. The only probable explanation of this condition is that these sporangial walls have been removed by a process of absorption or degradation in order to liberate the spores which, unlike those of the living Equisetums, are not provided with other special means of being set free. If this explanation is correct, the masses of spores must have been held together in the later stages of their development solely by the nodal disks and their upturned fringes of broad peripheral bracts.

Fig. 16 represents a lateral view of the lowest node and internode of Mr. BUTTERWORTH's original specimen, from which the section, fig. 1, was taken. I presume that the vertical ridges separated by furrows indicate the contours of a corresponding number of marginal bracts. Fig. 17 represents the concave under surface of the same specimen,* the concentric inflections of which evidently represent those of a nodal disk; most probably those of its inferior surface. In its centre, *a*, we see the fistular medullary cavity. Surrounding this we have at *i* an inner verticil of ten cortical lacunæ, identical with those seen at *i′* of fig. 1. Yet more externally we have twenty smaller lacunæ, *i″*, occupying the same positions as the two indicated by *i″*, *i″*, in fig. 1. The extreme regularity of these latter lacunæ is remarkable; the more so, because of their imperfect preservation in other sections. That they were normal features of the disk is shown by the section, fig. 18, which represents a fragment taken from fig. 17 and further enlarged. The two sets of lacunæ, *i*, *i′*, seen in that figure, are seen in fig. 18 to have well-defined contours suggestive of something more than accidental lesions. They obviously bear some definite relations to the sporangiophores, *l*, of fig 1, traces of which also appear at *l′*, *l′*, of fig. 18.

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* This was obviously not the lowest node of the strobilus.

Fig. 19 (Plate 9) is a radial section of a small twig or stem of a young Calamite, introduced for comparison with Plate 11, fig. 6. In this Calamite *b* is the medulla, *c*, *c*, internodal canals; *d*, a vascular bundle, and *d′*, the arching vessels of that bundle opposite the node *f*.

Having thus shown most of the details of the organisation of this strobilus from actual specimens, we run little risk of error in representing its morphology as seen in a vertical section by the restored diagram, fig 20 (Plate 9). The letters of reference are used in the same way as in the previous figures. The sections at *m′*, *m′*, show the inner and outer verticils of the sporangia only, having passed between two sporangiophores whilst at *l*, *l*, these sporangiophores are intersected vertically. The cortical lacunæ introduced at *i*, *i*, are omitted elsewhere for the same reasons.

The fact that so many specimens of these fruits, otherwise so rare, were aggregated in one small nodule probably indicates that they were borne singly upon the extremities of several small branches clustered round the extremity of one stem.

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8	2	Transverse section of a strobilus made through an internode: *a*, *b*, *c*, as in fig 1; *d*, vascular bundles; *k*, portions of the marginal bracts fringing the nodal disks; *l*, sporangiophores; *m*, *m′*, outer and inner verticils of sporangia. × 9. Cabinet, No 1583 .	49, 51, 52

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Plate.	Fig.		Pages on which references are made to the figures
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All the above references to the "Cabinet" indicate that each specimen so referred to will be found in my cabinet under the number assigned to it in the text. This cabinet will finally be placed in the Botanical Department of the Museum of the Owens College, where future students of Palæo-Botany will have free access to it. Whether such observers confirm my views or otherwise, they will have no difficulty in examining for themselves nearly all the specimens upon which those views have been based.

III. CROONIAN LECTURE.—*Researches on the Structure, Organization, and Classification of the Fossil Reptilia.*—II. *On* Pareiasaurus bombidens (OWEN), *and the Significance of its Affinities to Amphibians, Reptiles, and Mammals.*

By H. G. SEELEY, *F.R.S.*, *Professor of Geography in King's College, London.*

Received April 21,—Read May 12, 1887

[PLATES 12–21.]

THE genus *Pareiasaurus* was instituted by Sir RICHARD OWEN in 1876* for a large number of Reptilian remains from the Karroo Series of strata of South Africa. It was classed with the Dinosauria in a new family named Serratidentia,† and regarded as represented by two species, which were named *P. serridens* and *P bombidens.* Its place among the Dinosauria was held to be established by the teeth, which were compared to those of *Iguanodon* in their mode of implantation, and to those of *Scelidosaurus* in their close arrangement and nearly uniform wear, while the margins of the crown are similarly notched or serrate. The cranial characters are stated to concur with the dental characters in supporting the formation of a family in the Dinosaurian order for these fossils. Unfortunately the type-skull of *Pareiasaurus serridens* is now only known from a plaster cast, and by some small fragments cut from the lower jaw. The immense development of the so-called malar processes, which overlap the lower jaw and suggested the generic name, was regarded as showing a resemblance to the genus *Anthodon* from South Africa, and in a less degree to *Scelidosaurus* from the Lias of Charmouth. Regarding the fossil as a vegetable feeder, Sir R. OWEN remarked that the homologous descending malar process among Mammals is found only in those types which come nearest to Reptiles in brain structure, such as Kangaroos, Sloths, and Megatheroids.

In the cervical vertebræ sub-vertebral wedge-bones are found, which are likened to those which are said to occur in the fore part of the neck of Ichthyosaurs and Plesiosaurs. A notochordal canal penetrates to the centre of the centrum without piercing it, sometimes in a way almost Ichthyosaurian, but sometimes as a slender conical tube extending from the flattened articular face of the centrum. Sir R. OWEN remarks,* it is a trace of a lower grade of vertebral structure, and 'recalls the more widely perforated, still less ossified, centrums of the vertebræ of Ganocephalous Reptiles of the Carboniferous Series represented by *Parabatrachus, Hylonomus, Dendrerpeton,* &c.' The ribs are double-headed, with a parapophysial articulation on the centrum, a diapophysial facet on the neural arch.† The scapula and coracoid are said to be anchylosed together. The humerus is described as relatively broader than in *Omosaurus,* rather suggesting the breadth of the bone in the Mole The bone is solid Other parts of the skeleton are identified; but no further suggestions are made as to the organic relations of the type.

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* 'Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa,' 1876.

† In the 'Quarterly Journal of the Geological Society,' vol. 32, 1876, p. 45, the family is also named Tretospondylia, and made to include *Tapinocephalus* and *Pareiasaurus*.

About nine years ago the 'masons' in the British Museum, under the skilful direction of Mr. William Davies, F.G.S., removed the matrix from the skull and axial skeleton of an animal of this genus from Palmut Fontein, South Africa, sent to the Museum by Mr. Thomas Bain in May, 1878. The specimen (Plate 12) gives more ample and exact evidence of the nature of *Pareiasaurus* than was previously available, and renders a re-examination of its affinities convenient. I have undertaken this description in the belief that the structures of *Pareiasaurus* throw more light upon the evolution of the Reptilia than any fossil that has been described. And I would express my thanks to Dr. Henry Woodward, F.R S., Keeper of the Geological Department, for the facilities afforded me in making this examination.

The Head.

(Plates 13–16.)

The skull has the general contours of the head of a Frog, being broadly rounded in front, with the alveolar and jugal margins diverging posteriorly so as to form about two-thirds of an ellipse. The occipital border is transverse, and not evenly truncated. The upper surface of the head is flat, and the moderately deep post-orbital regions are obliquely inclined, so as to look outward and upward. The post-malar bones descend over the lower jaw in broader stronger processes than are seen in *Rhynchosaurus,* but differently shaped from those seen in Edentates. The head is widest over the inferior extremities of these processes, where the width is about equal to the length, which measures 45 centims.

The superficial bones, especially of the cheeks and upper part of the head, are sculptured with a pattern which combines radiating grooves of a Labyrinthodont type with Crocodilian pitting. In structure the skull, examined from above, is essentially Labyrinthodont; but, seen from the palatal aspect, it is altogether Dicynodont. The dentition is distinctive, but on the whole makes a close approximation to that of Dinosaurs. The right side of the head is in less perfect preservation than the left side, especially along the roof-bones, but the specimen has suffered no distortion.

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* 'Geol Soc. Quart Journ,' vol. 32, 1876, p 45

† 'Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa,' &c , 1876, p. 10.

I propose first to describe the nasal and orbital vacuities, then the structure of the external bones of the skull, and finally the palate and lower jaw.

The Nares and Orbits.

(Plates 13 and 14)

The nares are transversely and ovately elongated, but it is uncertain whether they were completely divided The transverse measurement over them is 15 centims., and the width of the premaxillary process which rises between them is 2 centims. where fractured. It is probable that the nasal apertures were conditioned much as in *Gorgonops*, in which the nasal bones approach the premaxillaries without forming a bony union with them. But in this fossil the nares are much larger than in *Gorgonops*, approach more closely together, and are less covered superiorly by the nasal bones, so that the vacuities look upward and forward. Each is about 4 centims. deep in oblique measurement from the concave posterior border on the nasal bone to the convex anterior border on the maxillary. But the vertical depth of the aperture is about 2 5 centims Their contours approach that of a figure 8 placed transversely The outer half of the inferior nasal border in the maxillary bone is channelled on its horizontal aspect with a broad concave groove 1·5 centim. wide, which ascends the ascending process of the maxillary bone and is limited externally by a sharp marginal ridge. Towards the median ascending process of the premaxillary bone the ridge dies away, and the bone is obliquely compressed so as to form a flattened area which looks upward and forward, and extends backward almost as far as the ascending premaxillary process, which rises almost vertically from it. There appears to be a bony floor to the nasal passage, but the bones are not in a condition to be determined ; and, though a part of the passage is exposed, it only shows, behind the premaxillaries, a small perforation, and a slight median ridge which appears to be vomerine. The nasal bone above the nares is compressed, and impressed on its external half by a broad canal which is fully 3 centims. wide This canal narrows as it ascends the convex nasal bone, and forms a deep groove with an elevated inner border, which is first directed backward, and then outward and backward, so as to terminate above the anterior angle of the eye, where it descends towards the orbital margin in a wide smooth expansion. I regard this canal as being the lachrymal mucus-canal, comparable to those of Labyrinthodonts, which are similarly placed.

The orbits for the eyes are placed laterally in the middle of the sides of the head. They look obliquely upward and outward, and very slightly forward. They are transversely elongated, 9·5 centims. long, are concavely rounded posteriorly, 5·5 centims deep in the middle, and pointed anteriorly, so that the outline is somewhat transversely pear-shaped. The anterior corner, which is inclined slightly downward, is 8 centims. behind the outer border of the narine; the space about it, and especially above it, is smoothed and somewhat impressed, indicating, I believe, remarks,* it is a trace of a lower grade of vertebral structure, and 'recalls the more widely perforated, still less ossified, centrums of the vertebræ of Ganocephalous Reptiles of the Carboniferous Series represented by *Parabatrachus, Hylonomus, Dendrerpeton,* &c.' The ribs are double-headed, with a parapophysial articulation on the centrum, a diapophysial facet on the neural arch.† The scapula and coracoid are said to be anchylosed together. The humerus is described as relatively broader than in *Omosaurus,* rather suggesting the breadth of the bone in the Mole The bone is solid. Other parts of the skeleton are identified; but no further suggestions are made as to the organic relations of the type.

About nine years ago the 'masons' in the British Museum, under the skilful direction of Mr. WILLIAM DAVIES, F.G.S , removed the matrix from the skull and axial skeleton of an animal of this genus from Palinut Fontein, South Africa, sent to the Museum by Mr. THOMAS BAIN in May, 1878. The specimen (Plate 12) gives more ample and exact evidence of the nature of *Pareiasaurus* than was previously available, and renders a re-examination of its affinities convenient I have undertaken this description in the belief that the structures of *Pareiasaurus* throw more light upon the evolution of the Reptilia than any fossil that has been described. And I would express my thanks to Dr. HENRY WOODWARD, F R.S., Keeper of the Geological Department, for the facilities afforded me in making this examination.

The Head.

(Plates 13–16.)

The skull has the general contours of the head of a Frog, being broadly rounded in front, with the alveolar and jugal margins diverging posteriorly so as to form about two-thirds of an ellipse. The occipital border is transverse, and not evenly truncated. The upper surface of the head is flat, and the moderately deep post-orbital regions are obliquely inclined, so as to look outward and upward. The post-malar bones descend over the lower jaw in broader stronger processes than are seen in *Rhynchosaurus,* but differently shaped from those seen in Edentates. The head is widest over the inferior extremities of these processes, where the width is about equal to the length, which measures 45 centims.

The superficial bones, especially of the cheeks and upper part of the head, are sculptured with a pattern which combines radiating grooves of a Labyrinthodont type with Crocodilian pitting. In structure the skull, examined from above, is essentially Labyrinthodont; but, seen from the palatal aspect, it is altogether Dicynodont. The dentition is distinctive, but on the whole makes a close approximation to that of Dinosaurs. The right side of the head is in less perfect preservation than the left side, especially along the roof-bones, but the specimen has suffered no distortion.

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* 'Geol. Soc. Quart. Journ.,' vol. 32, 1876, p. 45.

† 'Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa,' &c , 1876, p. 10.

I propose first to describe the nasal and orbital vacuities, then the structure of the external bones of the skull, and finally the palate and lower jaw.

The Nares and Orbits.

(Plates 13 and 14.)

The nares are transversely and ovately elongated, but it is uncertain whether they were completely divided. The transverse measurement over them is 15 centims., and the width of the premaxillary process which rises between them is 2 centims. where fractured. It is probable that the nasal apertures were conditioned much as in *Gorgonops*, in which the nasal bones approach the premaxillaries without forming a bony union with them. But in this fossil the nares are much larger than in *Gorgonops*, approach more closely together, and are less covered superiorly by the nasal bones, so that the vacuities look upward and forward Each is about 4 centims. deep in oblique measurement from the concave posterior border on the nasal bone to the convex anterior border on the maxillary. But the vertical depth of the aperture is about 2 5 centims. Their contours approach that of a figure 8 placed transversely. The outer half of the inferior nasal border in the maxillary bone is channelled on its horizontal aspect with a broad concave groove 1 5 centim. wide, which ascends the ascending process of the maxillary bone and is limited externally by a sharp marginal ridge. Towards the median ascending process of the premaxillary bone the ridge dies away, and the bone is obliquely compressed so as to form a flattened area which looks upward and forward, and extends backward almost as far as the ascending premaxillary process, which rises almost vertically from it. There appears to be a bony floor to the nasal passage, but the bones are not in a condition to be determined ; and, though a part of the passage is exposed, it only shows, behind the premaxillaries, a small perforation, and a slight median ridge which appears to be vomerine. The nasal bone above the nares is compressed, and impressed on its external half by a broad canal which is fully 3 centims wide. This canal narrows as it ascends the convex nasal bone, and forms a deep groove with an elevated inner border, which is first directed backward, and then outward and backward, so as to terminate above the anterior angle of the eye, where it descends towards the orbital margin in a wide smooth expansion. I regard this canal as being the lachrymal mucus-canal, comparable to those of Labyrinthodonts, which are similarly placed.

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The Premaxillary and Sub-narial Bones.

(Plate 14, fig. 1, *pm. in*)

The premaxillary bones are separated from each other by a median suture. They are narrow, and rise above the lower nasal border in an inter-narial process, which is fractured. There is no evidence which is quite conclusive as to the form and size of the bone. In the type-specimen of *P. bombidens* (British Museum Register, 43,525) I am clear that each bone only contains two teeth. But besides the suture, which extends obliquely outward, upward, and backward, giving an apparent superior width of 7·5 centims. to the bone, there is also a suture which ascends over the second tooth inward to the lateral margin of the ascending premaxillary process. These two sutures define a triangular plate, the apex of which descends between the second and third teeth, and the base of which extends along the narine. I regard this bone as a dermal plate, which hides the suture between the premaxillary and maxillary bones. It may be termed sub-narial, and is regarded as belonging to the same series as the supra-orbital, infra-orbital, and lachrymal bones of other animals. Professor W. K. PARKER, F.R.S., has described skeletal elements above the maxillary and below the nasal, forming a floor to the nostril, as characterising Urodeles and Anurous Batrachia, Varanian and other Lizards, and Snakes,* with which this ossification may, I think, be compared. In the specimen of *Pareiasaurus* now described, the structure of this region of the jaw is less clear, because the sub-nasal scale is so perfectly blended with the bones beneath, that its sutural limits are not very distinct. Hence the premaxillaries are narrow bones, formed on the Amphibian rather than a Mammalian type, which become narrower as they extend superiorly towards the nares. Their external surface is flattened, and retreats a little as it ascends, in harmony with the convex rounding of the snout. The fractured superior surface of the premaxillaries is oblong, having an antero-posterior extension of 4 centims. and a width of 2 centims. The teeth in its alveolar border differ in no respect from those in the maxillary bones. The palatal border of the premaxillary bones, like that of the maxillaries, projects downward below the palate so as to form an arch of bone within which the lower jaw is received.

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* 'Phil. Trans.,' 1878, p. 412.

The Maxillary Bones.

(Plates 13 and 14, *m.*)

The maxillary bones are moderately elongated, gently convex in length, and appear to contain 18 teeth on each side. Below the anterior corner of the eye the maxillary unites with the malar bone, which extends wedge-like into the middle of the maxillary, so that its anterior extremity has about five teeth below it in the posterior extremity of the maxillary, and there is a much shorter superior overlap of the maxillary upon the malar on the anterior border of the orbit. Measured round the curve, from the median premaxillary suture to the extremity of the sutural union between the maxillary and malar bones, the distance is 26 centims., and along the whole of this distance teeth are developed which are directed downward and inward. The maxillary bone is moderately deep, and has a strong ascending nasal process which is behind its middle portion and inclined a little posteriorly. It separates the orbit from the narine. The depth of the bone at the narine is 5 centims.; the depth at its posterior end is less than 6 centims. The least width of the ascending process between the anterior corner of the orbit and the external limit of the narine is 8·5 centims. The process is in a different plane to the rest of the bone, bulging anteriorly towards the narine, and retreating inward posteriorly towards the orbit. It extends upwards to the canal between the narine and orbit, along which the suture runs which divides it from the nasal and prefrontal bones. The vertical height from the alveolar border to the almost horizontal area external to the lachrymal canal is 10 centims. Round the middle of the external part of the body or dentary part of the bone is a row of large, distant, supra-dental, vascular foramina, which commence about 2·5 centims. above the alveolar border anteriorly, and descend to a height of 1 centim. posteriorly. At least six are seen which penetrate the bone as conical pits and vary irregularly in diameter from 5 to 15 mm. This main mass of the bone is very gently convex from the alveolar margin upward, and shows no trace of the inflated longitudinal ridge which runs along the middle of the bone in the type specimen of *Pareiasaurus bombidens.*

The Malar Bone.

(Plates 13 and 14, fig. 2, *mr.*)

The malar or jugal bone is about 17 centims. long, convex from above downward, roughened with small tubercles in front, and rugose behind with a coarser ornament, which is in harmony with that seen on the whole of the cheek into which it enters. The bone is elongated, concave superiorly, and obliquely truncated posteriorly in the manner of the prow of a barge, hence, while the superior border is about 15 centims. long, the inferior border is relatively short, and does not exceed a length of about 11 centims. Inferiorly it does not quite reach the post-alveolar border of the jaw, being excluded by the attenuated posterior process of the maxillary bone, which underlaps it anteriorly; and posteriorly it is underlapped by the quadrato-jugal, which is similarly attenuated as it extends forward, and it just meets the maxillary bone. The oblique posterior suture which limits the malar bone is about 8 centims. long. Posteriorly the bone has the quadrato-jugal below it, and the supra-quadrate bone behind; its rounded superior hinder extremity penetrates slightly between the front of the squamosal bone and the base of the post-frontal, which forms the upper hinder border of the orbit. On the posterior superior border, wedged between it and the post-frontal there appears to be a small bone, imperfectly preserved, which enters the orbital border, which I regard as the post-orbital bone The depth of the malar below the middle of the orbit is about 5 centims, and it terminates anteriorly in a broad wedge suture which extends into the maxillary as far as the anterior angle of the orbit.

The Cheeks.

(Plates 13 and 14.)

Behind the orbits, the cheeks form a coarsely sculptured mass of bones which extend continuously from the squamosal to the quadrato-jugal, and from the post-frontal to the hinder border of the head. These cheeks have a length of at least 18 centims. and a depth of 18 centims. The left side has not been developed to show sutures distinctly, but on the right side they are strongly marked by the weathering of the specimen. The bones completely hide the quadrate bone from lateral view, more absolutely than in Ichthyosaurians and Labyrinthodonts The bony elements forming the cheeks are the same as form the cheeks in those orders of animals, and they are similarly arranged. There is a post-orbital bone at the back of the orbit between the jugal and post-frontal; the post-frontal bone, which is large, is placed at the upper hinder angle of the orbit, and meets the squamosal behind. Below the squamosal and behind the malar is the supra-quadrate, and below the supra-quadrate and posterior part of the jugal, is the quadrato-jugal bone.

The Quadrato-jugal.

(Plates 13 and 14, *qj.*)

The quadrato-jugal is a long wedge-shaped bone, 20 centims. in length, which tapers anteriorly to a point. Its superior border is in contact with the malar bone in front and the supra-quadrate bone behind by a suture which is nearly horizontal and approximately straight, but undulating It is this bone which causes the oblique downward descent of the cheeks over the posterior part of the lower jaw, and not the malar bone, as in *Rhynchosaurus* and *Scelidosaurus*, so that the analogy with Dinosaurs, which was based upon the supposed resemblance of that development to the downward growth of the malar in *Scelidosaurus*, cannot be sustained. The quadrato-jugal is fully 6 centims. deep posteriorly, but is slightly abraded; its posterior border is vertically truncated, about 6 centims. long, convexly rounded from within outward, and forms inferiorly a large convex knob. In the middle of the posterior part of the external surface of the bone there is a strong vertical ridge, the whole surface is pitted, but the rugosities are not very marked. The inferior border of the bone is nearly straight, and convex from within outward. The internal aspect of the bone is smooth, concave in length, and, so far as the development of the fossil from the matrix permits determination, apparently free from any connection with the quadrate bone, below which its entire depth extends The transverse thickness of the bone posteriorly is about 4 centims., but anteriorly the thickness is reduced to little more than half as much.

The Supra-quadrate or Supra-temporal Bone.

(Plates 13 and 14, *st*)

The supra-quadrate is a slightly irregular, obliquely oblong bone, with its principal extension in the antero-posterior direction, and the two pairs of sides sub-parallel, and the short pair inclined backward It is 10 centims. long by 6 centims deep. The free oblique posterior margin is thickened, and terminates in two large rounded knobs, which form the upper and lower limits, and are separated from each other by a transverse depression. A straight longitudinal suture divides it from the squamosal bone above, and a longitudinal suture which is less straight separates it from the quadrato-jugal bone below, anteriorly it abuts against the inclined posterior end of the malar bone. The external surface is flattened rather than flat, being undulated with a rugose thickening on the anterior third. It is ornamented with strong radiating ridges, which diverge from its inferior border; they are large rounded ribs, which subdivide, and are sometimes broken into pits: about seven ridges and their interspaces occur in a width of 6 centims. I have no evidence whether the bone is in osseous connection with the quadrate bone.

The Squamosal Bone.

(Plates 13 and 14, *sq*.)

The squamosal bone is bent at an angle so as to appear upon the roof of the skull as well as upon the upper posterior part of the cheek. The lateral portion of the bone is rather smaller than the supra-quadrate, upon which it rests inferiorly. It is 10 centims long and 5 centims. deep. The free posterior border is thickened, and rounded into a convex boss with an elevated border like those seen on the supra-quadrate and in a less degree in the quadrato-jugal. These three bones have their inclined posterior borders extending further and further back, the higher their position on the side of the cheek, making its posterior outline oblique, but the line is regular because the upper knob on the quadrato-jugal extends rather further back than the two similar rugosities below and the one above, which cause the margin of the cheek to terminate in a row of four mammillate knobs which are nearly equidistant. The external surface of the squamosal bone is marked with very strong ridges and pits, which descend obliquely forward. Its superior border is badly preserved, and the superior horizontal part of the bone is much broken away.

The Post-frontal Bones.

(Plate 13, *pt.f.*)

The post-frontal bones lie in front of the squamosals, and are angularly bent in the same way, so as to continue the anterior prolongation of the superior horizontal ridge which divides the roof of the skull from the cheeks. They form the superior hinder border to the middle of the orbit (Plate 14, fig 2, *pt*), where the bone is exceptionally thick, and roughened with large mammillate bosses superiorly. Posteriorly the bone is pitted and sculptured like the other bones of the cheek. It is about 7 centims. long and upwards of 4 centims. deep laterally, measuring from the superior angle to the malar bone. The superior horizontal portion of the bone is larger, and overlaps the parietal, but from the condition of the specimen its sutures are less perfectly defined (Plate 13). It is about 6 centims. wide, but is shorter, meeting posteriorly a forward extension of the squamosal, and being in contact anteriorly with the ill-defined supra-orbital bone.

The post-orbital bone is an ill-defined wedge between the post-frontal and malar. It is 3 centims. deep on the orbital border, and appears to be 4 centims. long, extending backward to a point.

The Roof-bones of the Head.

(Plate 13)

The bones which cover the upper part of the head and lie between the nares, orbits, and the angles of the squamosal and post-frontal form a shield which is flattened but for a wide, shallow, longitudinal concavity which lies between the lateral bulgings, above the orbital border, and an anterior prominence on the nasal bones. It consists of the nasal, frontal, prefrontal, supra-orbital, post-frontal, squamosal, parietal, supra-occipital, and epiotic bones. Owing to the right side of these roof-bones being more or less broken away, the extremely weathered condition of the posterior part of the shield, and the presence of some planes of vertical fracture through the bones, the accurate tracing of the sutures is a matter of great difficulty. Moreover the surface of these cranial bones is strongly sculptured with grooves and pits, which have a tendency to longitudinal arrangement in the middle region, and laterally have a tendency to diverge outward more or less at right angles to the lateral border. The distribution of this ornament, as well as of the bosses and tubercles into which the intervening ridges sometimes rise, occasionally helps to define the sutures, which mostly run over comparatively smooth tracts of surface

The Nasal Bones.

(Plate 13; Plate 14, fig. 2, *n.*)

The nasal bone is only preserved on the left side, and is not quite perfect on the internal border, while it has lost the anterior process which extended towards the premaxillary. Above the compressed anterior narial border of the bone, which is concave in length and extends outward and backward, the bone thickens on its inner two-thirds of width, and rises into a super-nasal nodular transverse crest; and there are some indications that a transverse shallow mucus-canal extended over the anterior extremity of the bone. The nasal bones meet the frontal bones (*f*) behind; the prefrontals (*pf*) and the posterior lateral angle of the maxillary bones (*m*) join them externally. There is no satisfactory evidence of a median suture between the bones. The posterior border has a general transverse direction, but the frontal elements extend slightly forward between the nasals in a very wide angle, and their hinder extremities extend back so as to form nearly a right angle between the frontal and prefrontal bones, and thus the form of the suture is a drawn-out and inverted W. The measurement from the posterior narial border to the posterior angle of the bone is little more than 7 centims. The median posterior extremity is 14 centims. behind the anterior extremity of the skull. The transverse measurement over the nasal bone from the maxillary to the median line of the skull is 6·5 centims.; but externally the nasal appears to extend under the ascending process of the maxillary bone.

The Prefrontal Bone.

(Plates 13 and 14, fig. 2, *pf.*)

The prefrontal bone has a well-defined contour, being broadly sub-pentagonal, with the base inward. It meets the maxillary bone below and externally, and the nasal and frontal bones internally, having its greatest inward extension at the angle between those bones. Its inner border diverges outward, and meets the supra-orbital bone above the middle of the orbit. It enters into the anterior portion of the upper part of the orbital border Its antero-posterior length is about 9 centims Its extreme width is 5 centims Its antero-lateral border is rounded, and extends along the lachrymal canal, its postero-lateral border, which extends along the orbit, is not quite perfect, but appears to have been thick, and most elevated posteriorly, with the external lateral surface vertical.

The lachrymal bone appears to have no separate existence, unless it is present as a perforated scale in the mucus canal

The Supra-orbital Bone

(Plate 14, fig. 2, *so*)

Owing to the broken condition of the superior margin of the orbit, the supra-orbital bone is very imperfectly defined, and its limits are not satisfactorily determined. It is apparently a narrow crescentic bone above the hinder part of the orbit, with its external and internal borders sub-parallel Internally it meets the frontal and squamosal, anteriorly it abuts against the prefrontal, and posteriorly, above the hinder angle of the orbit, it meets the post-frontal bone. Its length is about 7 centims., and its width, imperfectly preserved, does not exceed 3·5 centims It combines with the prefrontal to form an arched ridge above the orbit, and the shallow concavity of the frontal region is limited laterally by these supra-orbital ridges. I believe this bone to be correctly determined, but it may be a dismembered part of the post-frontal.

The Frontal Bones.

(Plate 13, *f*)

The anterior contour of the frontal bones is broadly rounded. Each meets the nasal bone in front, and the prefrontal on the antero-lateral border. The transverse width of the bones anteriorly was 11 centims., as may be inferred from the lateral measurement to the median line being 5·5 centims. The sides of the bone are a little constricted and sub-parallel. Posteriorly the frontal terminates in a transverse suture, which penetrates in a shallow V-shape into the parietals The post-frontal bone probably touches its posterior angle. In the middle line the antero-posterior measurement is 10·5 centims There is no conclusive evidence of a median suture, owing perhaps to the longitudinal sculpture of the bone; but I incline to believe that it was divided.

The Parietal Bones and Supra-occipital.

(Plate 13, *p*, *so*.)

Behind the frontal bones the preservation of the skull is such that, although the bones are made out with some difficulty, their exact limits are not easily traced.

The parietal bones were each sub-ovate, about 7 centims. wide and 9 centims long The anterior contours are convex, and the width of the bone is diminished by overlap of the squamosal

Behind the parietals is a strip of bone 4 centims. long, and which may have been 16 centims. wide ; its posterior border is broken A small median ossification extends between the hinder limits of the parietal bones in a wedge-shaped suture, so that in the median line its length was 5 centims , and it is as wide as long, but probably extended laterally to the epiotic bones. It may be the interparietal.

? *Epiotic Bones.*

(Plate 13, *e*)

Internal in position to the posterior angles of the squamosals and behind those bones is a pair of transversely oblong ossifications, 3 centims. thick, which have the external surface horizontal. Each extends the outer upper corners of the skull further backward than do the bones of the occipital region, and is conditioned like the so-named epiotic bone of Labyrinthodonts. As preserved it is 6 centims. wide by less than 5 centims. long. Its posterior border is rounded from above downward, and its inner surface is vertical.

The Quadrate Bone.

The quadrate bone is not seen. It would appear to have been a very short flattened bone, with a ball-like articular surface on the palatal aspect of the head, though its width may have had no necessary relation to the great width of the articular element of the lower jaw.

The Palate.

(Plates 15 and 16.)

The palate of the type-specimen of *Pareiasaurus serridens* was worked out, so far as the chisel could do it, with consummate skill, as far back as when Mr. HENRY WARBURTON was President of the Geological Society, but has never been figured or described. Sir R. OWEN's cast is in itself a work of great skill, and is now the only evidence of its character. In general structure it is suggestively Anomodont, but it differs generically from any type of the order hitherto described. (See Plate 16, fig. 1.)

First, there is a large oblong basi-sphenoid (*bs*) in the middle of the hinder region. Its sides, which are rather constricted, I shall show to have been formed by the pterygoids, and its base is channelled in the median line, with the depression deepening as the pterygoids converge inward. From the anterior margins of this pterygo-sphenoidal mass the pterygoids diverge outward, and soon subdivide into two processes, one of which extends obliquely backward (presumably to meet the quadrate bone), and the other process is prolonged outward and forward at right angles, so as to meet the malar region just opposite the termination of the maxillary Hence it is in the position of the transverse bone, but there is no evidence that it is a distinct ossification. The median union of the pterygoids terminates anteriorly in a concave excavation, from the anterior corners of which slender bones extend forward parallel to each other, diverging outward a little anteriorly. They occupy the middle third of the palate, and from their middle send a narrow process upward and inward, which probably formed a median symphysis. Anteriorly the bones unite in the median line, and from this union a bony bar diverges outward and backward so as almost to meet the anterior termination of the forwardly directed process of the pterygoid, with which it is directly connected by a ridge parallel to the jaw, but separated from it by a depression. Anterior to the lateral connection with the palatines the vomer is prolonged forward I infer that there were two vomerine ridges parallel to each other, as in the anterior part of the skull of *Dicynodon pardiceps* (OWEN), but the bones are somewhat distorted, and the ridge is only preserved on one side

In the figured specimen of *Pareiasaurus bombidens* (No. 43,525), the palate is only known from a transverse section through the median union of the pterygoid bones, which shows the width of the bones and their stout character, with numerous sharp asperities on the palatal surface, which there is some reason for believing to indicate parallel or sub-parallel rugose ridges (*pt. r.*), but, although at first sight they resemble teeth, there is no trace of dentinal structure, and I am aware of no evidence that would indicate a toothed condition of the pterygoid bone. (See Plate 15, fig. 2.)

In the specimen now described (Plate 15, fig. 1) the palate is much less perfectly chiselled out than was the case in *Pareiasaurus serridens,* and only shows certain characters of its hinder region, but these are exceptionally important because some sutures are seen.

The basi-occipital bone (*bo*) is fractured so as to display the ex-occipital bones anterior to it, and to prove that it was posterior in position to them. Enough remains of its form to indicate that it constituted a large ovate articulation well rounded and defined inferiorly, which was about 6 centims. wide and 4 5 centims. deep. So singular is its relation to the bones behind that it is more like a post-cranial ossification than a constituent element of the base of the skull, abutting against the concave surface of the bones behind by a well-marked suture, which is posterior in position to the hinder limit of the skull, while it overlaps those bones laterally and inferiorly, where it is limited by a deep and characteristic infra-condylar depression. There is a doubtful indication of a vertical suture or groove dividing the bones against which the basi-occipital abuts. The fact that the superior margins of these bones appear to rise and form the lateral boundaries of the foramen magnum leads me to identify them as the ex-occipital bones. There is nothing unusual in the inferior median union of the ex-occipital bones in South African Reptiles. The tripartite condition of the occipital condyle is seen in many Dicynodont skulls in the British Museum; as well as in the skulls of Chelonians.* But in the Dicynodonts the basi-occipital has already been received between the ex-occipital bones, so that they take part in forming the condyle, though their extension downward to the base of the skull is not less marked than in *Pareiasaurus.* The interest of this specimen consists in the evidence it affords that the basi-occipital bone is essentially an intercentral ossification at the back of the skull, which has become enlarged and blended with the skull under mechanical conditions If it had not been developed, or had not been in bony union with the skull, then the head would have terminated posteriorly in two occipital condyles formed by the ex-occipital bones, between which there would be an inferior notch. Such a hypothetical condition is so suggestive of the Labyrinthodont mode of union of the skull with the vertebral column, as to indicate a possible method of transition from the Amphibian form of occipital condyle to such a type as is seen in Chelonian Reptiles by the blending of a notochordal ossification with the head. If we consider the structure of an Amphibian skull, there can be no *à priori* difficulty from the fact that it would bring the ex-occipital bones to some extent into bony union with the basi-sphenoid; but the posterior pre-condylar surface of these bones, which is in front of the basi-occipital, appears to project posteriorly for 15 millims. beyond the basi-sphenoid

The basi-sphenoid (*bs*) is partially blended with the pterygoid bone (*pt*), and the prominent oblong bony mass at the back of the palate is about 9 centims. long. Its external or lateral surfaces are concave in length, so as to constrict the transverse measurement to 5 centims. towards the anterior end, but posteriorly the bone widens, attaining a transverse measurement of about 8 centims., and terminating in two parallel convex bosses which are below and in front of the occipital condyle. In *Dicynodon* and *Ptychognathus* the corresponding processes have a much greater development vertically downward, and are seen in many skulls to be formed partly by the ex-occipital bones, for tripartite sutures cross the processes and separate the ex-occipitals from the basi-occipital bone between them. There are some indications in this specimen, especially on the left side, that the ex-occipital bones descend to the base of the skull.

A deep median channel extends along the basi-sphenoid, which increases in depth anteriorly so as to separate the pterygoid bones which margin the channel, before they become transversely united anteriorly above it, as well as by converging at its sides; but there is no evidence whether this or any other palatal vacuity is to be regarded as the posterior nares,

From the outer posterior angles of the bony pterygo-sphenoid mass a line of suture extends obliquely forward and inward to the median line on the left side. There is a trace of this suture on the right side, on the external posterior surface, [illegible] defined anteriorly; and I take these characters to show that the palatal surface of the basi-sphenoid is a long triangle, narrowing from a width of 7 centims. posteriorly to a point anteriorly, and defined laterally by nearly straight sutures, separating it from the pterygoid bones which extend along its sides (Plate 15, fig 1).

Hence the posterior margins of the pterygoid bones are in contact with the basi-sphenoid in a way more comparable to that seen in a Chelonian than in any existing group of Reptiles, but Chelonians have no such deep notch behind the process which is given off to the quadrate bone.

The present specimen shows that the sides of the pterygo-sphenoid process, seen laterally, are concave in length and gently convex from above downward, with the lateral palatal margin on each side compressed into a sharp rounded ridge. Anterior to the basi-sphenoid the bones unite in the median line at the base of the median sphenoidal depression, but also form by lateral expansion of their palatal surfaces a median union. The anterior lateral pterygoid plates become somewhat expanded, and differ greatly in form from the contours seen on the cast of *Pareiasaurus serridens*, while I am unable to see any indication of the pterygo-quadrate process which is so distinct in that species, and so characteristic of Dicynodonts. It may still exist in the matrix, or it may have been removed by the chisel. The lateral plate of the pterygoid, however, is shown by the vertical section of the skull of Sir R OWEN's type-specimen to be greatly expanded transversely (Plate 15, fig. 2), and there is a similar transverse expansion in this specimen, while sub-parallel lateral ridges of like character are seen upon its palatal surface. There are some indications that a bony process diverges outward and forward towards the orbit, and that the rounded posterior margins of the median pterygoid vacuity are prolonged forward by the parallel pterygoid bones, but no structure of the anterior part of the palate is shown. If the main points of structure of the palate prove, as will be presently shown, to be Dicynodont, the characters in which the bones differ from those of the Anomodont group will prove to be Labyrinthodont.

The Lower Jaw.

(Plate 14, figs 1 and 2; Plate 15, fig. 1, *md.*)

The lower jaw is a broad horse-shoe shaped structure with the rami well rounded in front, where they are united by a vertical median suture; posteriorly the rami are not recurved. The position of the jaw is vertical all round the curve. The bone is nearly 7 centims deep. Each ramus, measured round the curves, has a length of about 34 centims. Its thickness varies from a maximum of about 5·5 centims. below the orbit to 3·5 centims. anteriorly. At the median suture (*m.s*) there is a slight increase in the thickness of the bone, especially at the infero-posterior angle of the symphysis, which is produced backward in a kind of talon. The inferior surface is rounded from within outward, and rather flattened. But the basal contour of the anterior end of the mandible is convex from side to side; and there is also on the base, in the antero-posterior direction, a postero-lateral convexity below the orbit, more compressed from side to side than the jaw above, which ends abruptly on each side, at about 12 centims. from the posterior articular extremities of the mandible. Thus the lower jaw is supported on a tripod of three inferior convexities Behind the superior lateral convexities the jaw becomes compressed, especially on the external aspect, and its depth decreases as it extends backward in a convex curve, by not being produced so far downward; while superiorly, at the posterior end, it expands laterally, both internally and externally, into the diamond-like articulation, which is 9 centims. wide and apparently as long (Plate 15, fig. 1).

The mass of the jaw is formed by the dentary bone. It extends further back upon the alveolar border than upon the inferior border externally, where it is defined by an oblique suture descending downward and forward over the thickest and most convex portion of the jaw. On the inner side of the jaw the dentary bone does not extend so far back, and the suture, which separates it from the splenial bone behind, descends obliquely downward and backward. The angular bone is received between these internal and external lateral flaps of the dentary bone, and it is the downward growth of the angular bone which forms the infero-lateral prominences on the mandible. This bone, however, is exposed for a short distance, being covered posteriorly and externally by the sur-angular. There is no conclusive evidence whether the angular extends backward behind the sur-angular, as seems probable, to support the articular bone. Externally there is an impressed transverse suture between the articular and sur-angular bones, which gives a convex character to the sur-angular and emphasises the external projection of the articular bone. There are no fontanelles in the jaw; and there is no evidence of its internal structure in this specimen But the example figured by Sir R. Owen shows that a great vacuity like that which is demonstrated in *Pareiasaurus serridens* by the vertical sections of the jaw (Plate 16, fig. 2) extended forward round the dentary bone, defined superiorly by the thick sub-dental plate which extends obliquely downward and inward from the outer to the inner side of the jaw. In *P. serridens* this vacuity is higher than wide. It is a typical Labyrinthodont structure.

The Teeth.

(Plate 15; fig. 1; Plate 16, fig. 2.)

The external surfaces and extremities of the teeth are not well preserved. In the upper jaw they are inclined inward so as to have their external surfaces directed almost horizontally. A part of this curvature may be due to distortion, but that it is partly natural may be inferred perhaps from the teeth being directed inward all round the jaw, from their being in no case separated from the alveolar margin, and from the maxillary teeth being directed obliquely inward in the type-specimen of

*P. bombidens.** None are well enough preserved to show whether the extremities of the crowns of the teeth were similarly serrated The external enamelled surface is similarly semi-ovate and rounded from front to back, but in several instances it is marked by a few slight vertical ridges. The bases of the crowns are nearly circular; each is about 1 centim. long and rather wider, with a large central pulp cavity which extends above the alveolar margin. The interspaces between the bases of the crowns are about 2 to 3 millims long, but the summits of the crowns, which become compressed from within outward, are apparently in contact. Some of the crowns are from 2 to 2·5 centimetres long.

In the lower jaw the teeth are directed more or less outward, but this is more obviously an accident of fossilisation than the inward direction of the teeth in the skull. The crowns of the teeth are vertically ribbed. The external alveolar margin rises higher than the internal margin.

No evidence has been adduced as yet concerning the relation of the teeth to the jaw, though Sir R. Owen compares it to the condition seen in *Iguanodon.* In *Iguanodon* the teeth are essentially in an alveolar groove, though on its internal surface there are vertical grooves for the teeth, which terminate at their bases in separate pits. The only material available for settling this question is the small fragment of the lower jaw of *Pareiasaurus serridens* which appears to have been cut from the head of the specimen which Mr. Bain presented to the Geological Society in 1838. Dr. Woodward, F.R.S., has had the kindness to have this specimen cut vertically through the interspace between two teeth, and this section shows the existence of a bony septum between the teeth, thus demonstrating that the teeth are implanted in sockets (Plate 16, fig. 2).

The vertical section figured by Sir R. Owen is remarkable for showing a successional tooth beneath a crown without any fang. The fang is present, however, in the successional tooth, and closed at its base; but the union between the crown and fang appears to have been of the kind seen in *Mosasaurus.* From the position of the successional tooth, interior to the tooth in use, it is probable that it was developed as in *Ichthyosaurus, Crocodilus,* &c., so as to be more and more within the fang of the pre-existing tooth as its growth increased; only in this case there is no trace of a fang to the tooth in use, from which it would follow that in the process of fossilisation the fang of the pre-existing tooth disappeared, while the fang of the successional tooth remained; or else, as I think more probable, that the fang of the old tooth was absorbed before the new tooth was fully grown, and that meanwhile the crown was held in its place in the jaw by a deposit of osseous cement, in which case the condition of dentition would make a transition between that of *Protorosaurus* and the Crocodiles.

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* 'Catalogue of Fossil Reptilia of South Africa,' Plate 8, fig. 3.

Comparison with the Skulls of the Types of Pareiasaurus serridens (OWEN) *and* P. bombidens (OWEN).

There do not appear to be any satisfactory dental characters to distinguish the described species of this genus from each other; and it seems to me that their differentiation must rest upon the form, proportions, and structure of the skulls. Although the head is singularly distorted in *P serridens*, there is, I think, sufficient evidence that it differed from *P bombidens* in being less depressed; that it was more compressed from side to side anteriorly, as shown both by the contours of the skull and of the mandible; that the post-orbital processes were much deeper vertically, in harmony with the greater height and narrower form of the head. The rami of the lower jaw are straighter, more compressed from side to side, so as to be relatively thinner, though the specimen is larger; and the more pointed form of the lower jaw is manifest. On the palate *P. bombidens* appears to have the pterygoid bones much wider. The specimens appear to show many minor differences; but, as very little is preserved of the skull of *P bombidens*, and *P. serridens* is only known from the cast of the distorted skull and fragment of lower jaw, no detailed comparison can be profitably pursued.

The skull which I have described agrees with *P. bombidens* in having the anterior extremity of the mandible well rounded, though in the new specimen it is relatively wider, and the whole skull appears to be relatively broader, and is certainly broader and less pointed than the restoration of the contour of *P. bombidens* given by Sir R. OWEN.* The suture between the rami, which is lost in the figured type, is here strongly marked. The maxillary bone of *P. bombidens* (No. 43,525) is relatively deeper, and carries a strong median longitudinal inflation, which divides the bone into superior and inferior portions, while the specimen described has the bone more rounded from the alveolar margin to the orbital margin, and has only a slight indication of the longitudinal ridge. The number of the teeth is probably the same in both specimens; but no tooth in the specimen described has the extremity sufficiently preserved to show whether it possessed the serrations seen in *P. bombidens*, and it exhibits, especially on the hinder teeth, a few slight vertical parallel ridges, suggestive of those on the teeth of some Dinosaurs, which presumably indicate serrations, though they are absent from the teeth of the type of *P. bombidens*, from which, however, the outer film of enamel has in most cases peeled off. The skull appears to have been similarly flattened above, but too little of the bone remains to show whether it resembled the specimen described. And the lower jaw is broken away below the subdental plate, so that no detailed comparison can be made between the two specimens. It is, therefore, quite possible that the differences in form of the snout and teeth may extend to other parts of the skull, but, with the evidence before me, I prefer to regard the skeleton now under description as referable to *P. bombidens.*

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* 'Descriptive Catalogue, Reptilia, South Africa,' Plate 8, fig. 3, a.

Comparison of the Cranial Characters with those of other Animals

If the teeth had been found without other evidence of the animal, or if the jaws had alone been found, it would have been a fair induction to have classed *Pareiasaurus* with the Dinosauria. There is no other ordinal group in which coarsely serrated compressed crowns to the teeth are found, unless *Echinodon* and *Macellodon* should prove to belong to the Lacertilia, as Sir R Owen suggests. But placed in sockets, with the crown apparently united to the jaw by bony cement, the fang becomes absorbed by the successional tooth rather in the manner of Ichthyosaurs and Crocodiles, in which the germ is commonly on the middle of the inner side of the fang. The dentition approximates to that of Crocodiles rather than to the other orders of existing Reptiles, the dense packing and lateral compression, as well as the development of distinct alveoli, being Crocodilian characters, though the attachment of the teeth is not Crocodilian.

Turning to the palate, an instructive comparison may be made with the skulls of many species of *Dicynodon* and *Ptychognathus*, from the same geological horizon in South Africa, as well as with the allied animals, which Sir R. Owen has grouped into the ordinal name Theriodontia.

I have made a reduced restoration of the palate of *Pareiasaurus serridens* (p. 97), and if this is compared with *Dicynodon* the differences which are most manifest are, first, that the quadrate processes of the pterygoid are directed backward, so that the angle between them and the sphenoidal mass is less opened; while, secondly, the pterygoid processes, which in *Pareiasaurus* diverge outward and forward, so as to reach the margin of the jaw, are in *Dicynodon* directed forward, so as (in most cases) to lap along the palatine bones. Otherwise the relation of the pterygoid bones is the same, with apparently the same union with the sphenoid, the same median connection, and the same concavity between the anterior median ends of the pterygoid, which is prolonged forward, so as similarly to separate the palatine bones; and some Dicynodonts have two premaxillary or vomerine ridges. Hence, bearing in mind the variations which the palate exhibits in the Anomodont order, I think it may be affirmed that if no part of *Pareiasaurus* except the palate had been discovered it would have been a sound induction to have inferred that the animal was an Anomodont. If the teeth had been met with subsequently, they too might have been accepted as Anomodont or Theriodont, for the group presents so many variations of dental condition that the further variation seen in *Pareiasaurus* would have been no anomaly. Among existing Reptiles the nearest resemblance in the palate, as already indicated, is seen in the Chelonians; but the true Dicynodont palate is more decidedly Chelonian in its structure than this genus, and this condition may eventually have some weight in determining the genetic relations of these organic types.

If we turn to the superior aspect of the skull (Plate 13), it is no more Dicynodont than Dinosaurian. And it has every characteristic of a typical Labyrinthodont skull, among which may be mentioned its broad flattened form and sculptured surface, the small premaxillaries, the long malar bone, the narrow parietals, and the well-developed supra-temporal, quadrato-jugal, and epiotic bones, not to mention the lachrymal canal, and the probable existence of the post-orbital bone; while all the bones are arranged and conditioned as in Labyrinthodonts. The only other fossil type to which any resemblance can be traced in skull structure is the Ichthyosauria. But, although the form of the skull and positions of the orbits and nares are so dissimilar, the presence of supra-temporal and post-orbital bones is an interesting resemblance to *Pareiasaurus*, because *Ichthyosaurus*, so far as I am aware, is the only other type with a single occipital condyle in which a similarly developed supra-temporal bone is present. To living Urodeles the skull shows no resemblance, except in the unimportant matters of form and the small size of the premaxillary bones.

How these resemblances of the head to different ordinal types which are referred to different classes of Vertebrates can be harmonised, is found, I think, to be materially elucidated by the structure of the remainder of the skeleton.

The Vertebral Column.

(Plates 12, 17, 18.)

The vertebræ are preserved in natural sequence in a straight line. No bone is missing from any part of the column, unless a few terminal vertebræ should be lost from the extremity of the tail. There are only 29 vertebræ, of which 18 are presacral, 2 sacral, and 9 caudal, so that the number of presacral vertebræ is about the same as in the Japanese Salamander, *Sibboldia*; but the number of caudal vertebræ is only one-third of those in that type. The earlier vertebræ are rather shorter in antero-posterior measurement than the dorsal series, the greatest length and largest size being attained in the lumbar region, beyond which the vertebræ rapidly become small in the tail. Intercentra, or intervertebral wedge-bones of crescentic form, are developed on the ventral aspect of the column, between the dorsal and caudal vertebræ. In the early cervical vertebræ they are anchylosed to the anterior margin and base of the centrum, but in the dorsal and caudal regions these bones are free. The base of the centrum is compressed laterally in the earlier vertebræ into an inferior median ridge, which is moderately prominent, but disappears lower down the column, when the base of the centrum becomes rounded from side to side.

The ribs from the first articulate by double heads, which in the cervical region are upon the centrum made by the extremities of long forks to the cervical rib (Plate 17, fig. 1). The attachments of the dorsal ribs are partly on the neural arch, partly on the centrum; and the attachment to the centrum continues to rise higher, as far as the lumbar region. In the dorsal region the ribs are attached in a peculiar way, which can only be compared among Reptiles to the Crocodilian plan, but is distinct in type, having articulation with a relatively long parapophysial element from the centrum, and with a diapophysial element from the neural arch.

The neural arch is relatively broad and depressed, and carries an unusually short and massive neural spine (Plate 12, fig 1).

The entire length of the vertebral column is 197 centims., or about 6 feet 1½ inches, of which 50 centims. are in the neck, 83 centims. in the back and loins, over 15 centims. in the sacrum, and about 48 centims. in the tail.

The Cervical Vertebræ.

(Plates 12 and 17.)

I count all those vertebræ as cervical in which the parapophysial articulation for the rib does not rise appreciably above the level of the side of the centrum, and the vertebræ thus characterised are nine in number.

The first centrum is not quite perfect at the anterior end, so that it is impossible to say whether it possessed a regularly concave atlantal cup for the reception of the basi-occipital. As preserved, the centrum is short, being about 4 centims. long. It had prominent rounded margins to the intervertebral articulation. The anterior face as preserved is concave, and appears to have been cupped like the atlas in *Ichthyosaurus*, but the matrix has not been removed from the centre to show whether the notochord was persistent. The width of the superior part of the anterior face was about 10 centims.; its depth was about 8 centims. A double-headed rib was attached to this vertebra.

The neural arch is depressed and greatly produced anteriorly, and diverges outward at its anterior corners, as do the pre-zygapophyses of succeeding vertebræ, and these processes may have served to defend the sides of the basi-occipital bone. The anterior contour between these processes is concave; and the long lateral contours to the post-zygapophyses are constricted. The length of the arch is about 10 centims.; at its posterior extremity, on a level with the posterior articulation, there was probably a very small neural spine, now broken away. There is a small rib-like bone near the anterior process of the neural arch.

The second and third vertebræ both have the centrum about 5 centims. long. The second has a sharp median ventral keel, which is almost lost in the third, where it becomes a rounded ridge. In both the hypapophysial bone in union with the pre-articular basal margin of the centrum is relatively small. In the second it is sub-triangular, about 3 centims. long and as wide anteriorly; in the third it is cordate, retaining its width, but shorter posteriorly and rounded. These bones cover much of the basal ridge of the second vertebra. The sides of the centrum are concave from back to front, but above the middle of the side is a longitudinal ridge, strongest anteriorly, which bounds the impressed facet for the rib. On the right side the inferior process of the rib is still in contact with this facet. This process is 18 mm.

wide, somewhat compressed, and attenuates as it extends backward; its length is 4 centims. The superior process appears also to articulate with the centrum; it is half as long as the inferior process, is compressed from side to side, is as high as long; it is separated from the lower head by a well-marked notch more than 1·5 centim. wide. The length of the rib, which attenuates to its free end, is about 14 centims.

The attachment of the neural arch to the centrum is not seen. The form of the arch viewed from above is remarkable, and has an aspect of leaning forward to terminate in a short, large, truncated neural spine, which is ovate in section and compressed from front to back. Below the flattened slightly convex summit the neural spine is constricted a little from side to side, and then diverges outward and backward in strong, rounded, V-shaped, neurapophysial ridges, which enclose a posterior concavity between the zygapophyses, having a slight median ridge below the neural spine. The width of the neural spine is 5 centims. The width over the posterior extremities of the transverse processes is 10 centims ; the under sides of these processes carry the post-zygapophysial facets, which, however, are not seen in these vertebræ.

The centrum is larger in the fourth cervical, having a length of 6·5 to 7 centims. The intercentral ossification is more flattened, and the base of the centrum is more flattened. The tubercles for the ribs are larger, and elevated a few millimetres above the side of the centrum. The inferior head of the rib, which is still in contact with the centrum, is very massive, and fully 4 centims. deep. The neural arch of this vertebra is not preserved. In the fifth vertebra the centrum is shorter, being only 4 5 centims. long, while in the sixth it measures 6·5 to 7 centims., and in the seventh 7·5 centims. From this point, posteriorly, all down the dorsal series, the base of the centrum is lost, owing to the bone having been removed by a horizontal fracture of the rock in which the specimen was contained. The sides of the centrum, however, now become more constricted in the transverse direction behind the lower tubercle for the rib; the transverse measurement, which was 6·3 centims. in this position on the third centrum, is 5·6 centims. on the fourth and fifth, 5·4 centims. on the sixth, and 4·8 centims. on the seventh, in which the process for the attachment of the rib extends up the whole side of the centrum from a short distance above its base, and gives an aspect of semi-cylindrical excavation to its side. The spines on the neural arches are now all broken away, but appear to have become more vertical; the broken section is triangular. Anteriorly a slight median ridge extends forward, and divides the neural arch, so that the lateral surfaces diverge from it convexly outward and backward. From the anterior corners the pre-zygapophyses extend forward and outward as large sub-circular facets about 3 centims. in diameter. The transverse width over the pre-zygapophyses is about 18 centims., but at the second vertebra the transverse width over the post-zygapophyses is only 9·5, so that the neural arch becomes rapidly wider as it extends backward. There is a broad lateral constriction between the zygapophyses. The eighth vertebra has lost its neural arch, and is fractured through the centrum, and there is no conclusive evidence whether it should be counted as cervical or dorsal; still, as the skeleton appears to have divided naturally into its several regions, except that the last dorsal is in the same block of rock with the lumbar and sacral vertebræ, it may be that the first eight vertebræ are rightly accounted cervical, though the transition from the neck to the back may have been graduated as among Plesiosaurs. The articular bases of the later cervical ribs are rounded and circular with sharp margins, external to which there is a marked constriction of the shaft. There is no proof that the ribs in any cervical vertebra articulate with the neural arch.

The Dorsal Vertebræ.

(Plate 12; and Plate 18, figs. 1, 2.)

The dorsal vertebræ are nine in number. The first eight have been chiselled from the hard matrix as a slab which displays the bodies of the vertebræ and dorsal ribs on one aspect, and the neural arches and ribs on the other. In these vertebræ the base of the centrum is in every case lost. Transversely wide intercentral ossifications are seen between the third and fourth dorsal vertebræ, between the fourth and fifth and the seventh and eighth, but probably existed between all, and have been lost in the other intervals with the base of the centrum. Where I begin counting the dorsal vertebræ the transverse process for the lower head of the rib has already risen high upon the side of the anterior margin of the centrum. The head of this horizontal parapophysial process is expanded, and its articular surface flattened; its under side is compressed into an inferior ridge, and its dimensions contract like a neck to its junction with the centrum. It has a slight direction forward as it extends outward. At first the length of the process is about 2 centims., but in posteriorly succeeding vertebræ it elongates, and from the third to the eighth its length is about 3·2 centims. There is apparently no difference in the relative sizes, lengths, or position of these processes, and all terminate at their articular ends in the same straight line. The process on the ninth vertebra is similar. The interspaces between the bodies of the vertebræ are nearly 2 centims. wide. The sides of the centrum are constricted—4·5 centims. wide in the middle—and form as preserved vertical semi-cylindrical channels; but in the later dorsal vertebræ this hollow half-cylinder is inclined backward as it extends downward, and in the seventh and eighth centrums there is a manifest convergence of these lateral surfaces downward and inward, tending towards a rounding of the base of the centrum, which is perfectly rounded in the ninth and in the lumbar vertebra, and was, therefore, probably rounded throughout the dorsal series. The centrum is wider posteriorly than anteriorly; the sixth is less than 9 centims. wide anteriorly and 9·5 centims. posteriorly, but in the early dorsals there is no difference—both articular margins measuring 8·5 centims. in width.

The intercentra were limited to the ventral surfaces of the vertebræ (*i c.*). None appear to have exceeded 3 centims. in width or 6 centims in transverse length, but the preservation is so imperfect that no details of their characteristics can be given, beyond saying that in the anterior vertebræ they appear to lie well within the interspaces between the centrums, resting equally upon the basal margins of each adjacent pair; but in the posterior half of the dorsal series the posterior vertebra appears to contribute a larger surface for the support of this ossification, which gives the centrum an aspect of leaning obliquely forward. If this crescentic ossification were to become blended with either the anterior or posterior vertebra adjacent to it, the articulation would in the one case have a tendency to be procœlous, and in the other to be opisthocœlous; but, even though the co-ossification has not taken place, there is a tendency to the opisthocœlous condition in the lumbar vertebra

Seen from the dorsal aspect, the forms of the neural arches are distinguished by their great transverse width as compared with the antero-posterior extent; by the short, massive, neural spines (*n.s*), which, though of the same type as in the cervical vertebræ, become wider and wider posteriorly; by the outward and backward divergence of the nearly horizontal post-zygapophysial ridges; and by the way in which the diapophysis for the rib (*d*) is given off as a process cognate with the post-zygapophysial ridge, separated from the post-zygapophysis by a sub-ovate notch, and bounded anteriorly by a straight transverse line. Since the vertebræ are all in natural contact, the contour of the pre-zygapophysis is not seen. The chief differences in the neural arches as they extend down the back are that the neural spines become successively wider and more circular, and that the post-zygapophysial ridges elongate a little, while the angle between their diverging posterior borders becomes a little wider.

In the first dorsal vertebra the arch is badly preserved. It, however, shows that the diapophysis was rather short, so that the notch between it and the post-zygapophysis is wider than in succeeding vertebræ. On the left side the extremity of the post-zygapophysis is broken away, showing the pre-zygapophysial facet below as sub-circular, 4 5 centims. wide, nearly horizontal, but slightly convex from front to back. It is continuous with the anterior border of the transverse process, beyond which it extends as a thin plate. Hence the neural arch extends outward and forward in a wedge, and carries the circular pre-zygapophysis at its anterior corners (*pz*). This wedge is divided into two unequal and dissimilar regions by a transverse depression of the surface of its anterior half. This separates it from the post-zygapophysial ridge, which, somewhat narrower and more elevated, ascends up to the side of the neural spine, but in the later dorsals it is thrown a little further backward towards its posterior aspect and rises higher towards its summit. The neural spine is about 5 centims. long, and at the eighth vertebra is 4·5 centims. wide, though narrower anteriorly. Its superior surface is slightly convex, but flattened. As it descends to merge in the expanded neural arch it experiences a sub-conical contraction in size; its anterior margin is 3 centims. high, its posterior margin 4 centims. high There is an anterior ridge on the earliest neural spines, which is lost on the last dorsal vertebra, though the corresponding posterior ridge is continued to the lumbar vertebra, and behind the post-zygapophysial ridges the spine is a little compressed. In no case does the summit of the neural spine rise more than 2 centims above the post-zygapophysial ridge. The lateral measurement from the centre of the neural spine to the extremity of the post-zygapophysis is 12 centims. in the third dorsal vertebra, giving a length of about 10 centims to the zygapophysial ridge. The transverse width over the vertebra from one post-zygapophysis to another is fully 22 centims. in the early dorsals and 26 centims. in the late dorsals The measurement from the anterior margin of one post-zygapophysis to the posterior margin of the next is fully 13 centims., and from the posterior margin of one zygapophysis to the posterior margin of the next is about 9 centims. Hence the neural arch is nearly three times as wide as the centrum is long, and about twice as wide as the neural arch is long.

In no case is the articular extremity of a diapophysis of a dorsal vertebra exposed, so that there is no direct evidence of the nature of the division which separates it from the parapophyses.

The Dorsal Ribs.

(Plate 12.)

The ribs are in their natural relations of contact with the vertebræ, except that in the greater part of the series they are displaced slightly downward. Thus it happens that the diapophysis is seen to be transversely ovate, enlarging as it extends outward to the sharp edge of the articular surface, which is about 3·5 centims. long and 2 centims. deep in the earlier part of the dorsal series, but is deeper in the later dorsal vertebræ. The preservation of the ribs is very imperfect. Seven are seen on the left side, and six on the right side, but there can be no doubt that the ribs were as numerous as the dorsal vertebræ and comprised nine pairs.

The ribs are strong, enlarged at the proximal end, where the bone expands in the vertical direction on the ventral aspect. The anterior surface of a rib is convex from above downward; and the posterior side is incised with a deep median groove, most marked in the earlier ribs, which corresponds to the division between the articular heads, and does not extend far down the rib.

There is a slight antero-posterior compression of the diapophysial tubercle, which accentuates the oblique attachment of the head of the rib which results from the parapophysis being on the anterior margin of the centrum, while the diapophysis is rather more posterior in position. As preserved, the ribs have their dorsal aspect horizontal, and are compressed from above downward at a distance of about 8 centims. from the diapophysis, where the transverse measurement is about

2·5 centims. and the vertical measurement diminishes posteriorly. The ribs are directed outward horizontally, but soon curve backward.

The second dorsal vertebra shows on the anterior face of the proximal end of the rib evidence of a mode of articulation with the centrum which may be termed sub-Crocodilian. The head of the rib, which unites with the parapophysis, is prolonged for about 5 centims. beyond the articular surface for the diapophysis, which is transverse to the direction in which the rib extends. In the later vertebræ, in which the position of the head of the rib is more nearly vertical, the parapophysial process is some centimetres longer than the diapophysial articulation, so that the head of the rib is obviously notched (Plate 18, fig 1, *p*) in a way that is only to be compared with the early dorsal ribs of Crocodiles, though the vertebral elements which form the articulation are different. At the sixth dorsal vertebra the transverse measurement over the diapophyses is 21 centims., and over the parapophyses is 16 centims, which gives a mean elongation of the parapophysial head of 2·5 centims.

The ventral aspect of the rib is concave in length from within outward, and convex from front to back; it is somewhat constricted for a few centimetres external to the articulation; and when it widens, the expansion results from the anterior margin forming a sharp ridge, which, as in Crocodiles, is less prominent after extending for a few centimetres

It is impossible to form any estimate of the original length of the ribs, since the longest fragments preserved measure only 18 centims.

In the last dorsal the rib appears to be almost entirely supported upon the diapophysis, the parapophysis having become very small.

The resemblance in form which these ribs exhibit is quite as striking with types like *Anthracosaurus* and *Ichthyosaurus* as with Crocodiles and *Teleosaurus;* and in some Labyrinthodonts the ribs are probably as long as in Crocodiles, so that the shortness of the ribs in existing Urodeles throws no light on the ribs of *Pareiasaurus.* No remains of abdominal ribs are preserved.

The Lumbar Vertebra.

(Plates 12 and 19.)

This vertebra has the lateral constriction of the centrum rather more anteriorly placed than in the dorsal series, and these lateral surfaces round on to the base, which is convex from side to side. The posterior end of the centrum is expanded laterally to a width of 11 centims., and terminates in a sharp margin, which overlaps the first vertebra of the sacrum. Anteriorly its width is 10 centims. Its margin is convexly rounded, especially on the base, from which the thin intercentral ossification is lost. The intervertebral foramina between this vertebra and the last dorsal are higher than wide. The transverse process or lumbar rib is compressed from above downward, and at its base is produced anteriorly along the entire extent of the length of the ninth dorsal centrum, and directed slightly upward. Its antero-posterior extent is about 8 centims. The bone is directed outward and curves slightly backward, with all the characters of a lumbar rib. It is compressed from above downward, is 2 centims. thick, flattened above, rounded on the anterior and posterior margins, and convex from front to back on the ventral aspect. It extends beyond the anterior expansion, which rapidly contracts to a width of 4 centims., with sub-parallel straight sides, its extension being in a line with the interspace between the lumbar and the last dorsal. The neural spine is large and circular.

The Sacrum, Sacral Ribs, and Pelvis.

(Plate 12, *sm*, *sr*, *i*; Plate 19.)

Two vertebræ are anchylosed together in the sacral region, but only the first contributes to the support of the pelvis. The centrum is appreciably smaller than in the last dorsal and the lumbar vertebra; and the neural arch is more depressed, for the post-zygapophysial ridges of the earlier vertebræ have disappeared, and the arches are as completely blended as the bodies of the vertebræ.

The anterior face of the centrum of the first sacral vertebra is expanded, being about 10·5 centims. wide; it is in too close union with the lumbar to permit the form of this surface being seen. On the ventral border it retreats posteriorly just as does the lumbar, but there is no evidence whether this condition was dependent upon the development of a small sub-vertebral wedge-bone. Immediately behind this anterior border the lateral and ventral surfaces of the centrum diminish somewhat in size; and, though the constriction follows the same general plan as in the lumbar vertebra, its posterior limit is not expanded to the same extent on account of the anchylosis, for the greatest transverse measurement between the two centrums is about 8 centims. This less expansion at the anchylosis gives a more cylindrical and relatively longer appearance to the second sacral vertebra. And in form there is much in common between this centrum and the early caudal vertebræ. The height of the lumbar vertebra, from the base of the centrum to the summit of the neural arch, is about 19 centims.; the corresponding height of the first sacral is about 17 centims., and of the second sacral about 13 centims. The transverse width of the post-zygapophyses in the lumbar vertebra is about 21 centims.; here it is 9 centims. Thus, with the change to the sacral region, there is a marked decrease in the height of the centrum, the width of the neural arch, and the height of the neural spine.

The length of the sacrum along the neural canal is nearly 16 centims., but along the base the measurement would scarcely exceed 12 centims. The posterior articular face was slightly oblique. The neural spine of the first sacral vertebra measures 6 centims. from front to back, and is 5·5 centims. wide. The posterior median ridge upon the spine is very slightly developed, and there is no trace of the wide furrows which occupy the halves of the posterior aspect of the lumbar neural spine. The neural spine in the lumbar vertebra inclines slightly forward; here it is inclined slightly backward. In the second sacral vertebra the neural spine is much smaller, the antero-posterior measurement being 4 centims., while the transverse measurement is 4·6 centims, and the neural arch has diminished in size to the proportions of an ordinary Saurian vertebra. Very little remains of the transverse process and sacral rib in this vertebra, but it was compressed from above downward, expanded on the anterior margin at the proximal end, and formed on the same plan as the caudal ribs and the lumbar rib, though very much smaller than the latter, and but for the anchylosis there would be no character to separate the vertebra from the succeeding caudal series. The transverse processes extend the under side of the first sacral vertebra to a width of 13 centims. They are massive ossifications which extend along three-fourths of the side of the centrum and have a height of 8·5 centims from the base of the centrum to the neural platform. The process is directed outward and backward, and is only 3 or 4 centims. long, but is continuous with the sacral rib, from which it is divided by suture.

The sacral rib (*sr*) has a massive and extraordinary development, and is the only support for the pelvis. The bone is compressed from front to back, with its superior and inferior borders concave, so that it is constricted from a depth of 10 centims. at its junction with the transverse process, to 8 centims. at a distance of 5 centims. from that junction. The transverse width of the sacral rib on the ventral aspect is 19 centims. As the bone extends outward from the vertical constriction its plane twists to a more oblique position, which causes the mass of the bone to extend posteriorly, and to reach back to the level of the second caudal vertebra.

The anterior external angle of the rib is broken away. It was relatively thin, and was overlapped superiorly by the ilium (*i*); and it is not quite clear that it extended as far forward as the ilium. Its external border, which is inclined downward and backward from the level of the neural canal, had an antero-posterior extent of probably about 25 centims, though the posterior part of the bone now left in contact with the ilium along the external border is only half as long. The anterior aspect of this rib is flattened, being gently concave from within outward, and smooth, with slight indications of blunt ridges in its anterior outer angle. The infero-posterior border of the bone is well rounded from front to back, but the anterior edge is compressed, and bordered by a sharp anterior angle. As the bone extends outward it thickens in its posterior half to about 9 centims. on its junction with the ilium, which is received into a groove between the thin inferior expansion of the sacral rib and a strong vertical internal thickening. When seen from above and behind, the posterior 14 centims. of the rib seem to be received into a deeply concave recess in the internal face of the ilium, above which the sacral rib develops a strong tubercle, and anterior to which there is a long foramen, imperfect in front, of which only 6 centims.

are preserved. In front of the foramen the bone thickens, and is extending transversely outward towards the anterior corner of the ilium where it is fractured.

On the posterior side, near the junction of the sacral rib with the centrum, is a longitudinal groove like that already described in dorsal ribs, but relatively less deep, and soon lost as the bone expands outward.

The transverse width over the pelvis at the outer limit of the sacral ribs restored was about 44 centims.

There is no existing Reptile with similarly massive neural spines ; and only among the great Salamanders, like *Sibboldia*, is there anything comparable in shortness, stoutness, and sub-cylindrical character, but in that Amphibian the summit and centre of the spine is a conical cartilage, which remains unossified.

In the large Salamanders the connection between the single sacral vertebra and the ilium is made by an immense sacral rib, which is compressed from front to back, and is similarly wider than deep, so as to have a transversely oblong form.

The only group of Reptiles in which there is a similar development and attachment of the sacral rib for the support of the ilium is the true Dicynodonts, always supposing that the pelvic bones attributed to that type are rightly referred; and I am aware of nothing against the view taken by Sir R. OWEN of their association with Dicynodont skulls.

The ilium of *Pareiasaurus* was inclined to the vertebral column at an angle of 45°; it was chiefly elongated in an antero-posterior direction with its extension forward and upward from the acetabulum. The larger part of the bone lies behind the attachment to the sacral rib. The external surface of the ilium was sub-parallel to the longitudinal axis of the vertebral column. As the bone extends anterior to the acetabulum for the femur (a) it assumes a Mammal-like expansion. Its inferior border extends forward and outward, and the plane of the bone at the same time turns from the vertical, obliquely inward and upward as it extends forward, ending in front in a compressed plate about 2 centims. thick. If the form of the bone is Mammalian, its connection with the one sacral vertebra is a condition as strikingly Mammalian as Amphibian. It is a Mammalian resemblance that the bone lies almost entirely in advance of the acetabulum, while in the Amphibian *Sibboldia* the ilium is directed downward from the sacral rib and slightly forward. In various Mammals, from the Ratel and Glutton down to the Echidna, there is a vertical compression or depression or notched appearance of the bone above the acetabulum, in front of which its blade expands in a vertical direction as it extends forward.

As preserved, the length of the ilium is 40 centims. The posterior 12 centims. appear to be narrow from side to side, but this appearance may be partly due to state of preservation. The bone is convex from side to side superiorly above the acetabulum. The part of the acetabulum which lies in the ilium, concavely excavates the postero-external part of the bone, and forms a cavity 10 centims. long and 6 centims. wide anteriorly. The pubis and ischium are not preserved, but the marks of their attachment are seen on the inferior face of the ilium, stretching round the acetabulum in a crescent having an attachment which is from 3 to 4 centims. wide. The inferior internal or visceral margin of the ilium is convex from front to back, and there is a corresponding convexity externally in front of the acetabular border, where the bone is 11 centims. wide on the inferior aspect, so that there is a certain approach to symmetry between the external and internal surfaces; for the sacral rib prolongs the curvature inward anteriorly with a contour similar to that which the external surface takes in front, making a triangle, wide anteriorly, with concave sides which converge backward to a width of 9 centims. in front of the acetabulum. Very little of the under-side of the ilium is exposed, since the ischium and pubis covered the whole area behind and around the acetabulum, and the sacral rib underlaps the bone anteriorly except along a narrow external strip less than 3 centims. wide. On this inferior border, in advance of the acetabulum, a strong narrow groove curves forward for 9 centims, parallel to the rounded angle of the external margin. The greatest depth of the bone as preserved, measuring from the acetabulum to the nearly vertical crest of the bone, is 15 centims, and from the crest to the antero-inferior border is 12 centims. The superior crest is at least 18 centims. long; posteriorly, it thickens on the inner side, and its transverse measurement is nearly 3 centims.; in the middle it is 2 centims. thick, while anteriorly it widens considerably, but its superior border is broken away. The sacral rib extends to within 16 or 17 centims of the hinder extremity of the bone, and joins the middle of the ilium for about 16 centims, without rising into union with the superior crest of the ilium

The transverse measurement from the middle of the sacral centrum to the anterior corner of the ilium is about 31 centims ; but the plane of the middle of the acetabulum is about 9 centims. nearer to the middle line of the body. Thus the extreme width of the pelvis is 62 centims., and the width at the femoral articulation was about 44 centims.

The Caudal Vertebræ.

(Plate 12; and Plate 18, figs. 3, 4.)

The tail vertebræ diminish rapidly in size, and are noticeable for showing no trace of the notochordal condition attributed to this genus by its founder. In the earlier caudal vertebræ the flat articular surfaces of the centrum are in closer contact than in the later part of the series, as though their movements had been constrained by the extension of the pelvis parallel to them. The thickness of the matrix which separates the early centrums is only about 2 millims.; and this close contact may have caused the early caudal vertebræ in the pelvis, attributed to *Dicynodon*, to be classed as sacral. But in the pelvis of *Pareiasaurus*, even the second sacral vertebra might, theoretically, be termed sacro-caudal, since it resembles the caudal series in form, and takes no part in supporting the pelvis.

All the caudal vertebræ have the ventral aspect of the centrum convex from side to side, but the convexity diminishes in the hinder part of the series, because the transverse processes, which at first are just below the level of the neural canal, gradually descend lower on the side of the centrum in the later vertebræ of the tail. The margins of the articular surfaces of the centrums are sharp and moderately elevated. The antero-posterior measurements of the centrums are, for the first, 6·3 centims.; the second, 5·4 centims.; the third, 5 centims.; the fourth is slightly shorter; the fifth, 4·5 centims., the sixth, 3·6 centims.; while the seventh and eighth are still shorter, but their bases are so obscured by wedge-bones that the measurement cannot be definitely given. The ninth is only preserved as a fragment, and may not have been the last vertebra, since the neural arch is well developed in the eighth, in which transverse processes are present, though small.

In the earlier caudal vertebræ there is a slight compression of the sides of the centrum below the bases of the transverse processes, which were separate ossifications united by suture to short tubercles from the centrum. These caudal ribs are mostly broken away, and it is only in the sixth, seventh, and eighth vertebræ, in which they are small and rapidly diminishing in size, that the free extremities of the processes are seen. They are horizontal, and are directed outward and backward. The longest fragments have a flattened lath-like form, but are only 6 centims. long. The origin of the process on the centrum is as wide as the centrum is long. Anteriorly its superior angle descends from the front of the pre-zygapophysis, and is marked by a sharp ridge which carries the base of the process forward and helps to define an anterior concave area between this zygapophysial ridge and the tubercle on the centrum to which the base of the costal rib is attached. Hence these ribs have the appearance of being attached to both the neural arch and centrum. After the second caudal, in which the transverse width of the base of the caudal rib measures about 6 centims., its antero-posterior extent diminishes, being 3·5 centims. on the third caudal, and 2 centims. on the sixth caudal. In the fourth to eighth caudals the base of the process is nearly as wide as the centrum, and is sub-quadrate, and the process itself is sub-cylindrical, terminating outward in a rounded hemispherical extremity. In the sixth vertebra the process is about 7 centims. long, in the seventh about 4 centims. long, and in the eighth 3 centims. long. In these vertebræ the size of the rib so rapidly attenuates that its anterior border is convex and the posterior outline concave; while the riblet, when seen from the front, is wedge-shaped.

Between the ventral margins of the earlier caudals there is no trace of a wedge-bone; but the intercentrum between the fifth and sixth takes the form of a disc. Between the fifth and sixth it is a small ossification in the median interspace, about 3 centims. in transverse extent. Between the sixth and seventh vertebræ the bone is less than 2 centims. long and about 4 centims. wide, and encroaches on the borders of both adjacent vertebræ. In the succeeding interspace the bone consisted of right and left portions like chevron bones, of which the left, which is alone preserved, is prolonged backward and constricted posteriorly, so as to be, though fractured, 3·3 centims. long. From the last interspace both these ossifications are gone.

The neural arch is characterised by wanting the post-zygapophysial ridges which are so strikingly developed in the dorsal region. The neural spines are broken away from all the vertebræ except the first; but they appear to have been more compressed from front to back than in any other region of the column, and to lean backward. The first caudal neural spine measures 5 centims. from side to side and 3·3 centims. from front to back, so as to be tranversely ovate. The free superior extremity is slightly larger than the shaft of the spine, which is about 4 centims. long. The spine forms much of the mass of the neural arch. Down its anterior median line a slight ridge extends, which is prolonged forward in the median line between the pre-zygapophyses, defining two lateral areas, which are sub-horizontal, and bordered by concave outlines between the zygapophyses, which are prominent laterally. The neural spine is at the hinder angle of the neural arch as in Urodeles, and the post-zygapophyses project from below its hinder lateral limits. The transverse width over the zygapophyses of the third vertebra is about 7·3 centims., which is equal to the width of the centrum, so that the abnormal width of the arch in the dorsal region is here lost. The posterior contour between the post-zygapophyses is concave. The arch continues to diminish in width towards the end of the tail, in harmony with the reduced size of the centrum, but it becomes better defined laterally by the constantly lower position of the costal rib, so that after the first three vertebræ there begin to be lateral areas slightly inclined, but almost vertical, between the inter-zygapophysial ridge and the transverse processes. The superior surface of the caudal neural arch has a flattened aspect of leaning backward. The height of the fourth centrum to the small circular neural canal is about 4 centims.; the transverse width of the neural arch above the transverse process at the end of the caudal series is 4·5 centims. The pre-zygapophyses look upward, inward, and slightly forward.

The Shoulder Girdle.

(Plates 12 and 20.)

The massive bones of the shoulder girdle are thrust in between the skull and the atlas. They are imperfectly preserved, and consist of an inter-clavicle and clavicle which unite by suture; and the anchylosed coracoid and scapula, which are more massive than the ilium, but are preserved imperfectly.

The inter-clavicle and clavicles form an anterior or bow-shaped arch which is formed on the general plan of Nothosaurians and certain Lizards. The inter-clavicle is in the median line in front, and is a symmetrical V-shaped bone, with its limbs widely diverging and directed backward. The median anterior extremity was thickened, convex, and inclined slightly downward, but has a truncated aspect, as though broken, or as though forming a boss which helped to support the body when at rest. This surface is transversely ovate, 5 centims. wide, and nearly 4 centims. long. The antero-posterior extent of the bone is about 11 centims. Its lateral arm extends outward and backward for 21 centims. from the anterior convexity. These arms are external to the clavicles (*cl*) and beneath them, and thin away posteriorly. On the flattened inferior surface of the bone, which is concave from side to side, a sutural line extends transversely outward, so as to make each half of the border slightly concave, which divides the inter-clavicle from the clavicle. On the internal or superior aspect the entire width of the clavicles is exposed so that they almost meet in the median line as they rest upon the inter-clavicle; and their convex anterior borders fit into corresponding posterior concavities on the posterior side of the bone. Anteriorly the bone is nearly 5 centims. thick, and becomes thinner behind. The anterior border is straight, and rounds somewhat sharply into the external surface; while, as it ascends in a convex curve over the oblique anterior aspect of the anterior border of the clavicle, the median anterior aspect of the inter-clavicle is convex from side to side.

The clavicles are compressed flattened bones, with their external contour convexly curved as it extends backward, and the external and internal borders sub-parallel. Both bones are imperfectly preserved, but the longer one measures 38 centims.; it is about 8 centims. wide in the middle, and becomes narrower towards both extremities, so that the curvature of the convex external margin is greater than that of the concave internal margin. The anterior median extremity of the bone is rounded from within outward. A transverse section (Plate 20, fig. 3) shows that the bone (*c*) is received as a wedge between superior and inferior flanges of the inter-clavicle (*ic.*); the bone is thickest in the middle, and thins towards the posterior margin. The transverse width over the posterior ends of the clavicles was probably about 50 centims.

On the ventral side of the left clavicle are imperfect remains of the scapular arch, formed, it may be presumed, of scapula and coracoid, blended at the humeral articulation, on both sides of which the bone extends. The humeral articulation was probably transversely oval, measuring 14 centims. by 9 centims., and was remarkably shallow in its concavity (*g*).

At right angles to one extremity of this articular surface is a compressed sheet of bone, less than 2 centims. thick and fully 8 centims. wide, which extends as preserved for 12 centims. beyond the articulation. This may be the precoracoid. At the other end of the articulation, the scapula first contracts in dimensions, and then is prolonged as a massive shaft, sub-ovate in section, which at the fracture is fully 10 centims. from front to back, and about 7 centims. from within outward. What I take to be the internal surface is smooth and unbroken, and similar to the external surface, the only difference apparently being that there is a notch, which appears to extend obliquely through the bone just in advance of the articulation. This structure is approximated to in some Anomodonts from South Africa.

Armour.

From the analogy of *Belodon* it might have been anticipated that the enlargement of the extremities of the neural spines of the dorsal vertebra would be correlated with the support of a weighty mail of dermal plates. But the form of the spines is more suggestive of Urodeles, in which no such armour exists. No indications of large dermal bones are preserved, and they probably did not exist, since small dermal bones lie in the interspaces between the post-zygapophysial ridges. They are irregular in form, and vary in size and thickness, though they are mostly about 7 millims. thick and are thinner at the margin. The external surface is nearly smooth, though it is slightly keeled in one case. Several plates are 3 5 centims. wide, and were probably sub-quadrate. There is no evidence that they were in close contact with each other. Smaller scutes are found above the sacral vertebræ, and also above the early caudal vertebræ.

Other Remains referred to Pareiasaurus

Sir Richard Owen referred to *Pareiasaurus bombidens* many other bones from the same locality, Vers Fontein, which yielded the type-skull. I am not concerned to discuss the grounds on which this reference may have been made, because no evidences of their relation to the skull are offered. The bones are described as a cervical vertebra, a dorsal vertebra, "the coalesced humeral ends of the right scapula and coracoid," the right and left humeri, the right ulna, the right ilium and portion of the left ilium, and proximal portion of the right femur.* Another bone, from Jan Willem's Farm, also referred to this species, is the right tibia; and some vertebræ from this locality are referred to *Pareiasaurus* without the species being determined. These remains, with the possible exception of a vertebra, are proved by the foregoing description to belong to a different genus.

First, the "anchylosed scapula and coracoid" (No. 43,525) are manifestly the anchylosed ischium and pubis. If any difficulty were felt as to this determination, it is removed by fitting the anchylosed bones to the ilium, when the surfaces perfectly correspond and show the bones to complete the pelvic structure of one individual (Plate 21, fig. 1). The type of pelvis, as shown by the ilium, is as different from that of *Pareiasaurus* as the ilium of a Seal is unlike that of a Bear; and, as it is also attached chiefly to a single sacral vertebra, and unlike in form the ilium referred to *Dicynodon*, or *Platypodosaurus*, or any described South African fossil, it probably indicates an undescribed genus. There is a strong enough resemblance to those types to leave no doubt that the animal was an Anomodont. It would be inconvenient to enter now into a detailed discussion of the structure of this type, which may be designated *Phocosaurus megischion*. The pelvis furnishes the only element of the skeleton, except the vertebræ, which can be compared, and I therefore offer a brief account of this region in justification of the present interpretation which separates it from *Pareiasaurus.*

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* Figured, Owen: "Description of Parts of the Skeleton of an Anomodont, &c.," 'Geol. Soc. Quart. Journ.,' vol. 36, Plate 17, fig. 8.

The pelvis of *Phocosaurus* (Plate 21, fig 1) is remarkable for the enormous size of the hemispherical acetabular cup for the femur. More than half of the acetabulum is made by the ilium, and its lower portion is made up in nearly equal parts by the pubis and ischium, which are united to each other by a straight suture. The pubic bones were probably united with each other by suture in the median line of the body (Plate 21, fig 2); but, owing to imperfect preservation, there is no evidence of the relations of the ischiac bones to each other.

The antero-posterior width of the acetabular cup is 25·5 centims.; its vertical height is more than 23·1 centims. The cup is broader below than above, and is so placed that the iliac portion overhangs the part formed by the other bones.

Superiorly within the acetabulum the ilium forms a horizontal, ovate, articular surface, which is rugose as though lined with cartilage; it is 14 centims. long by 9 centims. wide. Its presence greatly thickens the ilium, and I infer the plate to have been developed by supporting the femur in terrestrial movements. And, as this plate is narrower than the acetabulum, I judge the head of the femur to have been smaller than the acetabulum. This superior articular surface is defined anteriorly by a long deep groove, which extends backward from its anterior corner. The iliac surface in the acetabulum below this groove appears to have been a smooth surface, which took no part in supporting the movements of the femur; it is more than 10·2 centims. deep to the sutural union with the pubis, while the corresponding depth posteriorly to the ischium is 3·8 centims. Posterior to the superior articular surface is a corresponding concavity, but the groove is less developed. The transverse width of the inferior border of the ilium is 29·2 centims., divided into two nearly equal parts inclined to each other in a broad V-shape. The contour of this transverse sutural surface for union with the inferior pelvic bones is a crescent, concave from front to back along the acetabulum, convex along the visceral surface. The sutural surface is transverse to the external surfaces; its greatest thickness at the outer limits is 6·3 centims., while its transverse measurement in the middle is only half as much, so that the acetabular cup is part of a smaller circle than the more flattened curve of the visceral surface. Necessarily there is a corresponding difference in breadth of the pubis and ischium.

Superior to the acetabulum, both the anterior and posterior contours of the ilium are constricted to a width of 16½ centims.; the posterior concavity is the narrower curve from above downward. The external aspect of the bone is convex above the acetabulum, but the convexity diminishes as the bone widens superiorly. Vertically from the superior margin of the acetabulum to the superior crest of the ilium the bone is concave, owing to the crest curving outward. Owing to the increased height of the crest of the ilium, the depth of this part of the bone is greater in front than posteriorly, but is fully 20·4 centims. in the middle.

Anteriorly the bone is imperfect in both examples But the curvature of the superior crest in the right ilium as it extends anteriorly leads to the conclusion that the anterior prolongation may not have been greater than the elongation of the posterior angle. So far as I am aware, this is the only example of an Anomodont Reptile in which a distinct posterior process to the ilium is developed. As preserved, the antero-posterior extent of the ilium below the superior crest is about 30½ centims , but I infer the bone, when complete, to have measured 38·1 centims.

The superior crest, which is otherwise thin and sharp, thickens posteriorly, and develops a sharp ridge 7·6 centims. from the posterior extremity of the bone. The whole of the posterior side is thickened from within outward.

The ilium is supported chiefly by one sacral rib, which has a large union with the bone, and a transverse width of 20 to 23 centims. On the right side there appear to be at least two more small ribs in contact with the posterior process of the ilium.

The form of ilium is about intermediate between that of an Ornithosaur (Plate 18, figs. 5 and 6) and the ilium of a Seal (Plate 21, fig. 3).

The pubis and ischium are anchylosed or closely united by a straight vertical suture, so as to form a strong elongated bony plate, which is imperfect posteriorly, owing to fracture of the ischium. As preserved, the antero-posterior measurement in the middle of the united bones is 41 centims., of which the pubis contributes a length of 20 centims., to its junction with the ischium. The measurement downward and inward from the acetabular margin to the median ventral line of the body is 25 centims The plane of the bones is curved, so that the visceral aspect is concave from within outward, and the bones of the two sides of the body would form a semi-cylindrical trough: the transverse measurement from the median ventral suture to the suture with the ilium is about 27 centims. External to the comparatively narrow union with the ilium is the oblique contribution which these bones make to the acetabular cup. This surface is concave from front to back, measuring 25 centims. in length; and its width is 11·5 centims. anteriorly and 10 centims. posteriorly. This transverse measurement forms much of the acetabular thickness of the bone, which is 14 centims. at the pubis and nearly 13 centims. at the ischium. Both pubis and ischium are expanded and sub-quadrate in form, though the inner and hinder part of the ischium is not preserved. Below the acetabulum the attenuation in thickness is remarkable, especially in the middle, though the bones thicken laterally to some extent on the anterior margin of the pubis and the posterior margin of the ischium. These margins diverge from each other as they extend downward and inward, so as to lengthen the antero-posterior extent of the bones. The anterior pubic border includes three areas: first, below the acetabulum, is a concave border, smooth, and rounded from within outward; then the bone thickens a little to a rugged surface which forms a rounded angle; and then it extends transversely inward as a long, straight, rather compressed, cartilaginous surface (*p.p.*). This surface may have supported a pre-pubic cartilage. The posterior margin of the ischium is preserved for 18 centims.; it is slightly concave below the acetabulum, but is approximately straight as it extends inward and backward. It is smooth, perfectly ossified, and rounded from within outward.

The external surface of the ischium is comparatively flattened, while the surface of the pubis is irregularly concave. The pubic foramen (*f*) is 10 centims. from the acetabular margin, and an equal distance from the concave anterior border. Below the foramen there is a convexity.

A comparison with the pelvic bones already figured or preserved in the British Museum, and referred by Sir R. OWEN to Anomodonts and Theriodonts, demonstrates the generic distinctness of this type, not only from the ilium originally referred to *Pareiasaurus*, but from every other form. It is, however, necessary to state that the ilium, S. A. 122, described in the 'Descriptive and Illustrated Catalogue,' p. 70, is the specimen originally figured in the 'Transactions of the Geological Society,' vol. 7, Plate 34, figs. 2, 3, *sg.* It was then regarded as either a scapula or coracoid of *Dicynodon*, and it is remarked that, if it is regarded as a scapula, the bone which is represented in contact with it in fig. 2 and lettered *cp*, which is perforated like the ischio-pubic bone, is regarded as probably the coracoid, and likened to that of *Iguanodon.* In the Catalogue above referred to the former bone is regarded as the left ilium, but it is manifestly the right ilium, since the mass of the bone is always anterior to the acetabulum in these animals; the latter bone is certainly the anchylosed ischium and pubis, and the whole of the pelvic bones are likely to belong to species of *Dicynodon.*

The characters of the vertebræ referred to *Pareiasaurus* have been fully elucidated by Sir R. OWEN in his paper in the 'Quarterly Journal of the Geological Society,' and in the 'Catalogue.' They are proved by the short centrum, small neural arch, different attachment of the ribs, and relatively longer and more slender neural spine, not to belong to *Pareiasaurus.*

On the Nature of the Relation of Pareiasaurus *to other reputed Dinosaurs from South Africa.*

There are four reputed genera of Dinosauria from the Karroo beds of South Africa. Professor HUXLEY, in 1866, described *Euskelesaurus* and *Orosaurus;* and, although no figures were given, the description leaves no room for doubt that the systematic position of those fossils was well determined. This is not the case with the genera *Anthodon* and *Tapinocephalus,* defined by Sir R. OWEN. If the affinities of an animal could be inferred from the teeth, there is so close a resemblance between *Anthodon* and *Acanthopholis* that there ought to have been certainty as to its place among Dinosaurs, except that the long fangs of the teeth are firmly imbedded in bone But although the skull is badly preserved, so that the sutures are made out with difficulty, enough is seen in the post-orbital region to show that the bones are arranged upon the Labyrinthodont plan which characterises *Pareiasaurus.* The quadrato-jugal bone is similarly formed, and descends below the level of the quadrate articulation. The region above the quadrato-jugal appears to include the malar, supra-temporal, and other bones. The vertebræ attributed to this genus have the neural arch expanded in a way that somewhat approximates to *Pareiasaurus,* but the centrum is as deeply cupped conically as in any Fish. The resemblances to *Pareiasaurus* are good evidence that both genera belong to the same group of animals, and better evidence of affinity than the form of the teeth.

Tapinocephalus is too imperfectly known from the extremity of the snout to furnish any certain evidence of its affinities or classificatory position. The head is apparently constructed on a distinctive plan, but the teeth are hollow, as in Labyrinthodonts, and have the fang imbedded in bone, as in *Pareiasaurus* and *Anthodon,* while the slight ridges on the crown are not unlike a few seen on some of the hinder teeth of *Pareiasaurus bombidens.*

I am not aware of any evidence which would justify the association of the skull-fragment with the vertebræ, which have already been described,* and differ from those of *Pareiasaurus* in not showing any hypocentral ossification.

The Affinities of Pareiasaurus.

The discussion of the regions of the skeleton described has shown that *Pareiasaurus* combines in one animal characters which are found in Labyrinthodontia, Reptilia, and Mammalia, and it becomes necessary to examine the significance of these resemblances. The investigation is beset with difficulty on account of uncertainty as to the nature of the skeleton in the larger Labyrinthodontia, the absence of knowledge of the limbs and preservation of *Pareiasaurus,* and the necessarily hypothetical interpretation, on such imperfect data, of the relations between classes of animals.

The Labyrinthodont Characters of Pareiasaurus.

The Labyrinthodontia have been usually grouped with the Amphibia, but there is some reason to believe that many different grades or varieties of organization have been comprised under this name which have no near relation to existing Amphibians. Dr. FRITSCH, after carefully describing the varied fauna of Stegocephali from the Permian rocks of Bohemia, concludes that, with our present knowledge, it is impossible to say whether the Stegocephali are Amphibians or Reptiles. The characters by which these organisms are related together are, first, a common structure in the roof of the skull, which is unknown in existing Amphibians and Reptiles; secondly, all the

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* 'Geol Soc. Quart. Journ.,' vol. 32, Plate 4, p. 43.

Labyrinthodont genera have a separate parasphenoid; but Dr. FRITSCH does not regard this as an important Amphibian characteristic, since the parasphenoid of *Hatteria* closely resembles the bone in the genera *Hyloplesion* and *Microbrachis*, and there is reason to believe that the bone is not united to the basi-sphenoid in the young of *Hatteria*, thirdly, Labyrinthodonts agree in the structure of the shoulder-girdle, but Dr. FRITSCH states that if the lateral plates of the breast armour are regarded as the coracoid bones, and the middle plate as the inter-clavicle, then the shoulder-girdle has more in common with a true Lizard than with an Amphibian. This is, perhaps, the most obscure and difficult point in Labyrinthodont structure; but it does not appear to me that either the Ichthyosaurian or Nothosaurian shoulder-girdles lend support to Dr. FRITSCH'S suggested interpretation.

Dr. FRITSCH attaches but little importance to the articulation of the skull with the vertebral column by means of two condyles, since two lateral condyles, formed by the ex-occipital bones, are present in the young *Hatteria* and in Chelonians; but it is stated that the basi-sphenoid* extends below them, forming a third condyle. This contention may deserve detailed discussion. The genera are grouped into four sub-orders, which are defined on the ground of vertebral structure, lengths of the ribs, presence or absence of gill-arches, and external resemblance to existing Amphibians and Reptiles. They are named Urodeloideæ, Gymnophioideæ, Saurioideæ, and Crocodilioideæ, but none of these sub-orders are identified as ancestors of existing Amphibians or Reptiles.

The difficulty in determining the systematic position of the Labyrinthodontia has been experienced practically by every student of the group, and, if its classificatory position rests upon the ossification of the gill-arches and the presence of a double occipital condyle, we must admit that the ways in which other parts of the skeleton approximate to structures in extinct and existing groups of Reptiles make the coincidences more suggestive of near affinity with the higher class. They may be technically Amphibians, and yet almost cover the interval between that class and the Reptilia.

I have long been led to regard the Labyrinthodontia as standing in an ancestral relation to the Reptilia, either of a direct or collateral kind, for many reasons. First, the changes of structure are simple by which characteristic portions of the skeleton in many Reptile orders could be derived from a Labyrinthodont type. Secondly, because the structural resemblances of several extinct orders of Reptiles with Labyrinthodonts are as remarkable as their resemblances with existing orders of Reptilia. Thirdly, because it is manifest that, if the descendants of Carboniferous and Triassic Labyrinthodonts have survived in existing Amphibia, they have undergone changes in their skeletons of as marked a kind as any changes which would be necessary to evolve Reptilian skeletons from the same types. I quite agree with Dr. FRITSCH in failing to recognise any very close relation between the existing Amphibia and the Labyrinthodontia; and, if I urge near affinity between the latter group and the more ancient Reptiles, it does not follow that there is as close an affinity between the more modern Reptiles and existing Amphibians, for the Amphibians have experienced structural changes akin to those which Reptiles have undergone, implying collateral descent.

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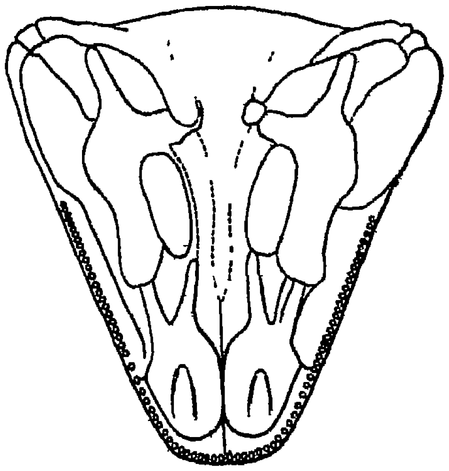
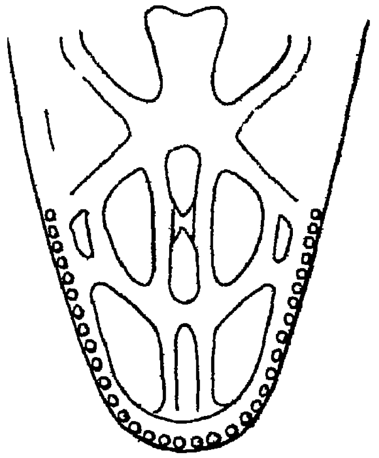
* This statement is repeated in the explanation of the figure, but I am aware of no evidence for questioning the identification of this bone as the basi-occipital.

It seems to me beyond question that *Pareiasaurus* is an animal in which there is transition from the Labyrinthodont to the Reptile exhibited in every part of the skeleton. The head shows five Labyrinthodont characters—(1) the form, (2) the sculpture of the cranial bones, (3) the arrangement of the bones which cover the head, (4) the presence of mucus-canals between the orbits and nares, (5) the absence of the lachrymal bone from the anterior corner of the orbit of the eye. The only difference on the upper surface of the skull from that of a Labyrinthodont is in the large size and close approximation or confluence of the anterior nares, which is a Reptilian character of some importance, as bearing on the mode of respiration.

The palatal surface is at first sight not so obviously Labyrinthodont, and the only genus of that order which I remember as showing any approximation to the palate of *Pareiasaurus serridens* is the Permian fossil *Nyrania* as restored by Professor Fritsch.* In so far as can be judged from these figures, there appears to be a certain correspondence of plan in the palate; and the condition of the bones in *Nyrania* is suggestive of the possible limits of the vomera, palatines, and pterygoid bones in *Pareiasaurus*. The differences from the Labyrinthodont palate are the absence of a distinct parasphenoid bone in *Pareiasaurus* (which is only conjecturally present in *Nyrania*), the presence of the basi-sphenoid on the palate, and the existence of a median palatal vacuity, in all of which characters there is rather a resemblance to embryonic stages in the development of the skulls of the existing Amphibia.



Nyrania



Pareiasaurus.

At the back of the skull the essential difference from a Labyrinthodont is in the presence of a single occipital condyle. How that condyle comes to be there, formed of one bone, and not contributed to by the ex-occipitals, is a theoretical question to which the specimen suggests only a speculative answer.

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* 'Fauna der Gaskohle, &c.,' vol. 2, Heft 2, p. 35.

The vertebral column of the larger Labyrinthodonts is imperfectly known; but the large intervertebral wedge-bones are characteristic of the group, and the biconcave centrum is equally characteristic, while the articulation of the ribs in the dorsal region by double heads to capitular and tubercular facets of transverse processes has been attributed by Professor HUXLEY to *Anthracosaurus.*[*] Similar vertebræ were figured by VON MEYER and PLIENINGER,[†] and referred to *Mastodonsaurus.* Both these types have more in common with *Pareiasaurus* than has *Loxomma,* in which the intercentra appear, from the description by Dr. EMBLETON and Mr. ATTHEY,[‡] to be as well developed as the centra. Whether the cervical, sacral, and caudal vertebræ would present in any Labyrinthodont the characters here described in *Pareiasaurus* there is not sufficient evidence to demonstrate; but the probabilities all incline towards that conclusion. Still the resemblance of the vertebral column to that of a Crocodile is so marked in the mode of articulation of the cervical and early dorsal ribs, as to leave no doubt that, while it approximates in plan to the Labyrinthodontia, it is equally close to the plan of the Crocodilia. The sacral region, as already observed in the description, is comparable with existing Urodeles in so far as its mode of union with the pelvis is concerned. There is an *à priori* probability that the pelvis in some Labyrinthodonts may have been attached in the same way; but, in the absence of knowledge of the pelvic structures of the larger Labyrinthodonts, it may be unsafe to attribute much importance to resemblances of an isolated kind to certain existing Amphibia. Therefore the coincidence of anterior direction of the ilium and a certain correspondence in its form between *Pareiasaurus* and anurous Amphibia need only be noticed for what they are worth; but the support of the ilium by a single sacral vertebra, through the intervention of a large sacral rib, is a character which implies Amphibian rather than Reptilian affinity. But that it is not the character of an Amphibian may be inferred from its presence in several genera of Anomodonts, and from the fact that in *Platypodosaurus,* which is of Anomodont type, the character is lost, and the pelvis is supported by a sacrum of several vertebræ in the manner seen in Dinosauria and certain Mammalia.

The inter-clavicles and clavicle are less markedly Labyrinthodont than other parts of the skeleton, and yet offer a sufficiently close resemblance in plan to show that the Labyrinthodont type has been modified, but not lost. The divergence which they show is rather towards the corresponding bones of the Nothosauria than to the clavicular arch of the Ichthyopterygia.

Hence I regard the conclusion as evident that, so much of the skeleton of *Pareiasaurus* as is preserved suggests that the genus arose from a Labyrinthodont ancestry. But, although there is a preponderance of Labyrinthodont characters in the skeleton, they are combined with other characters only found in Reptiles; and therefore the Labyrinthodont characters do not refer *Pareiasaurus* to the Labyrinthodontia. The type, which has lost but few Labyrinthodont characteristics, has yet some of the most striking characters of various orders of Reptilia, and it is upon these facts, which I now go on to state, that the conclusion must rest that *Pareiasaurus* and other Reptilia exhibit evidence that the Reptilia arose from the Amphibia by certain osteological changes which left the fundamental structure of the skeleton substantially the same in most of its parts.

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[*] Professor MIALL remarks that there is no proof that these vertebræ and ribs belong to *Anthracosaurus;* but there is no reason to question their Labyrinthodont character.

[†] 'Beiträge zur Paläontologie Württembergs,' 1844, Plate 4, fig. 6; 'Geol. Soc. Quart. Journ.,' vol. 19, p. 63, fig 2.

[‡] 'Ann. Mag. Nat. Hist.,' July, 1874, p. 57.

The Reptilian Characters of Pareiasaurus.

The Reptilian characteristics of *Pareiasaurus* which are not also common to the Labyrinthodontia are few. But they comprise some of the most remarkable characteristics of the Reptilia and of different Reptile orders; and the smallness of their number is evidence that they have been developed upon a basis of Labyrinthodont structure.

First, there is the large single, rounded, occipital condyle, formed of one bone. This has been taken as the test structure in classification, which not only separates the Amphibia from the Reptilia, but unites the orders of Reptiles together, and blends them into one group with Birds. The skull of *Pareiasaurus* exhibits no trace of ever having had two occipital condyles, and the articulation of the head with the vertebral column is as Reptilian as in any known order of Reptiles. If the two occipital condyles had been present, it would have been difficult to resist the conclusion, notwithstanding other characters of the skeleton, that *Pareiasaurus* was a Labyrinthodont; and therefore the presence of the single condyle, into which the ex-occipital bones do not enter, is the best osteological evidence that could be produced that the animal is a Reptile. There is necessarily no direct evidence as to the mode of origin of the condyle, but its development in a skull the external characters of which are so conspicuously Labyrinthodont may perhaps justify a consideration of a possible origin which the vertebral column of some Labyrinthodonts suggests. In various well-known genera, such as *Loxomma,*[*] *Diplovertebron,*[†] *Cricotus,*[‡] &c, it is well known that there are large intercentral ossifications developed which may in all respects resemble a centrum of a contiguous vertebra, except that the inter-centrum does not carry a neural arch. In *Pareiasaurus* such intercentral ossifications are present, but are of smaller size, and limited to the ventral portion of the centrums between which they are placed. If it is conceived that such an intercentral ossification were developed in the part of the notochord between the atlas and the skull, and blended with the skull in the same way that the atlas and axis are often anchylosed together, then the origin of the single basi-occipital condyle might be accounted for as the modification of a structure which was already foreshadowed in the axial skeleton.

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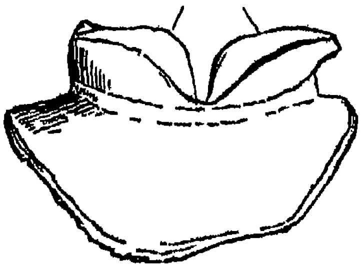
[*] EMBLETON: 'Ann Mag Nat Hist.,' July, 1874.

[†] FRITSCH: 'Fauna der Gaskohle,' vol. 2, Heft 1, Plate 52.

[‡] COPE: 'American Naturalist,' January, 1884.

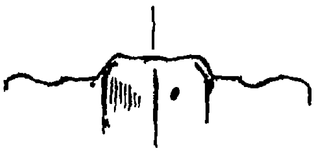
The single condyle would thus lose none of its importance as a mark of affinity between the animals in which it is found, but as the mystery of its existence disappeared it would be realised that the change from the Amphibian to the Reptilian mode of union of the skull with the vertebræ does not necessarily imply a wide difference in organization. It is interesting to remark that the body of the atlas is very short in the great majority of Reptiles, Birds, and Mammals, as it theoretically might be if its anterior half were incorporated with the skull. Some evidence in support of this origin for the single basi-occipital condyle is perhaps furnished by the fact that the bone is conspicuously large and rounded in the Ichthyopterygia, which preserve a larger number of Labyrinthodont characters than any other order of fossil Reptilia, while in Reptiles which have lost the technical distinctive marks of the Labyrinthodonts it enters further into the skull, and is received between the ex-occipital bones, though at first extending chiefly below them. Among the Anomodontia the basi-occipital bone is embraced laterally by the ex-occipital bones; the same condition, in a less striking degree, characterises the Chelonia; it is seen in the Plesiosauria, Teleosauria, Dinosauria, Rhynchocephalia, and among Birds. If the Reptilian and Avian form of occipital condyle could thus be derived from the Labyrinthodont type, the recurrence of the double ex-occipital condyles in the Mammal may be but the consequence of a still further forward movement of the basi-occipital bone, in consequence of which it has come to occupy a position analogous to that held among Labyrinthodonts by the basi-sphenoid. Such an appearance of forward movement of the basi-occipital would be a consequence of increasing size of the brain, tending to throw the basi-occipital bone into the floor of the brain-case. Hence it is possible that the condylar cranial characters may be related in an evolutionary sequence of gradation, and that the change from one condition to another may be consequences of one plan of Vertebrate organization rather than of entirely independent plans.

Exoccipital articulation.



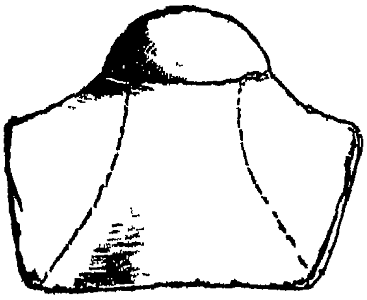
Mastodonsaurus.

Articulation



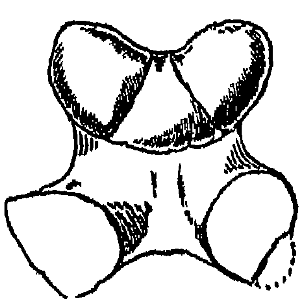
Seeleya.

Basioccipital condyle.



Ichthyosaurus

Tripartite condyle Basi-occipital between exoccipitals.



Dicynodon.

The other Reptilian characters of *Pareiasaurus* are shared by Anomodontia, Ichthyopterygia, Nothosauria, Plesiosauria, and Crocodilia; and it may be preferable to consider these resemblances separately, since they appear to me to lead to the conclusion that the several orders of Reptilia are developed from Labyrinthodont types, and have all preserved more or less of the original skeletal structures. And, if so, it must follow that they are related to each other, not as relatively higher or lower orders, which can be arranged in a vertical sequence, but as parallel groups variously modified upon approximately the same horizon of organization.* And their evidence will contribute to show that the Labyrinthodont characters of *Pareiasaurus* differ only in degree, and not in kind, from the structures of various Reptiles.

Resemblances to the Anomodontia.—Notwithstanding the many genera which this group includes, no complete skeleton is at present known, and consequently some uncertainty may attach to the association of vertebræ and other remains with the species of skull to which they have been referred, but I see no reason to question the determinations which have referred those pelvic, vertebral, and appendicular remains to the Anomodont order, and to the allied type named Theriodontia.

If the base and palatal aspect of any Anomodont skull, such as *Dicynodon leoniceps*† or *Oudenodon megalops*,‡ is compared with the palatal aspect of *Pareiasaurus* (p. 97), the resemblances are more striking than the differences. The basi-sphenoidal mass in both is of similar form, and is similarly concave longitudinally. In both it is blended with the pterygoid bones; in both it sends a slender process backward towards the quadrate, separated from the basi-sphenoid by a deep notch; in both there is a median union of the pterygoids in front of the basi-sphenoid, and a median vacuity in front of the expanded plate; in both there is a parallel pair of palatine bones extending forward: while in some species, like *Dicynodon pardiceps* § and *D. testudiceps*,‖ the palate terminates anteriorly in two parallel ridges like those seen in *Pareiasaurus*. The points in which differences can be detected all concern the anterior lateral part of the skull in the vomerine region, and the mode of union of the palatine bones. But the comparison shows a correspondence of plan which is compatible with both types belonging to the same ordinal group, and the resemblance is more remarkable than that which has been already indicated between *Pareiasaurus* and the Labyrinthodont *Nyrania*. And the correspondence seems to me of greater weight as evidence of affinity with Anomodonts than are the external resemblances evidence of affinity with Labyrinthodonts, because the remainder of the Anomodont skeleton shows an equally close correspondence with *Pareiasaurus*. The dorsal vertebræ referred to *Dicynodon pardiceps*¶ have a Plesiosaurian length of centrum with biconcave articular ends, such as Plesiosaurs exhibit in many species, but the mode of attachment of the rib is that of a Dinosaur, in the head of the rib being upon the centrum, and the tubercle upon the transverse process; but this condition is approximated to in the early dorsal vertebræ of Crocodiles and of *Pareiasaurus.* It is also found in vertebræ of *Mastodonsaurus*, in which the capitular attachment of the rib becomes elevated above the centrum, as in *Pareiasaurus,** but, owing to the shortness of the centrum in that genus, the resemblance to *Pareiasaurus* is not impressive, especially as the zygapophyses are not conspicuous for transverse expansion It may be that the difficulty in showing closer correspondence with the vertebral column of the Anomodonts is entirely due to the evidence not having been brought to this country, since the correspondence in the sacral region appears to be absolute. The sacrum referred by Sir R. OWEN to *Dicynodon tigriceps* may include only two vertebræ, though the succeeding vertebræ are in close apposition owing to the influence of the pelvis in limiting movement, and exactly the same condition is seen in the vertebræ of *Pareiasaurus,* which immediately follow the sacrum. The form of the centrums is essentially the same. in both the sacral rib of the first vertebra is similarly expanded so as to support the pelvis, and is similarly directed outward, backward, and downward so as to give attachment to the ilium along its oblique external margin. Moreover the ilium of *Dicynodon tigriceps,* in its ordinal characters of form, direction, and relation to the other pelvic bones, is essentially comparable with *Pareiasaurus,* and every other ilium of Dicynodont type from South Africa is constructed essentially upon the same plan. Hence it must follow either that the whole of these pelvic remains which have been referred to Anomodonts have nothing to do with them, and really belong to near allies of *Pareiasaurus,* or else *Dicynodon* and its allies so resemble *Pareiasaurus* in sacral and pelvic characters that only a generic difference in the form of the ilium can be used to separate them. Now, in view of the correspondences pointed out in the palate, and other resemblances in some characters of the vertebræ, there is no *à priori* improbability in pelvic and sacral resemblances between these two types, but, on the contrary, some reason for anticipating resemblances. And the weight of evidence seems to me to incline in favour of Sir R. OWEN's interpretation of the pelvic characters in the Anomodontia, rather than to support the induction from the extension of the characters of the Pareiasauria which might legitimately follow from my own account of its pelvic structure. This evidence may be appreciated by comparing the bones, or even wood-cut figures, like those which follow, in which representations are given of the forms of pelvic bones in Anomodonts from South Africa which have been described.

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* "Origin of the Vertebrate Skeleton," 'Ann. Mag. Nat. Hist.,' July, 1872, p. 44.

† OWEN, 'Descriptive and Illustrated Catalogue,' Plate 26.

‡ *Loc cit*, Plate 63.

§ *Loc. cit.*, Plate 38.

‖ *Loc cit*, Plate 44

¶ 'Descriptive and Illustrated Catalogue,' Plate 53.

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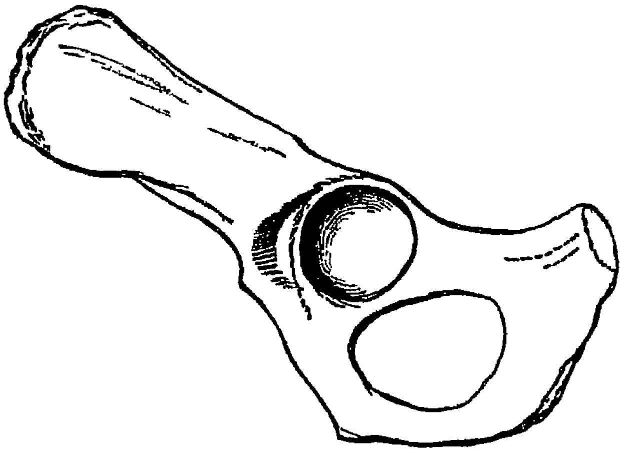
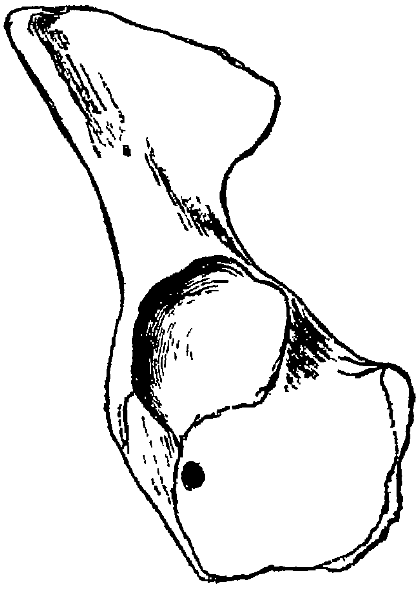
* VON MEYER and PLIENINGER, 'Paläontol. Württembergs,' 1844, Plate 4, fig. 6



Pelvis of *Ursus*



Pelvis of *Dicynodon leoniceps* (Ow.)

It is evident that the South African Anomodont Reptiles all have the pelvis formed on the same plan, which exhibits as many minor modifications (p. 107) as there are known groups of Reptiles in those rocks; and therefore I see no reason why we should hesitate to accept the other unassociated forms of ilium as rightly referred to the animals which have been grouped as Anomodonts and Theriodonts, and so recognize their near affinity with *Pareiasaurus*. But if this conclusion be legitimate it gives rise to another inference of some osteological importance, namely, that animals which possess closely similar pelvic structures may differ in cranial structures as much as *Dicynodon* and *Pareiasaurus;* but this will not seem improbable when we remember the history of the correlation of pelvic and cranial characters in the Dinosauria, Nothosauria, and Crocodilia, and the diverse crania which go with persistent pelvic structures. But, if the Anomodonts and *Pareiasaurus* are such near allies, it follows that the Anomodonts are also nearly related to the Labyrinthodonts, and that the covered skull of the parent Amphibian type has undergone processes of change comparable to those which Tortoises show when compared with Turtles, by which the head has lost the bones which are distinctly Labyrinthodont, and has become Reptilian. If there were reason to suppose that this change was exceptional to the Anomodontia, there might be reason to hesitate to admit it as a sufficient explanation of the persistence of Labyrinthodont characters in the upper surface of the skull in *Pareiasaurus;* but there is probably no order of Reptilia in which marked Labyrinthodont characters may not be traced in the skeleton, though they are more conspicuous in some orders than in others, and the validity of the explanation offered must rest upon the evidence that other orders of Reptiles, in which the skeleton is better known, show proofs of such transition as is inferred to have taken place in Anomodonts.

Resemblances to Ichthyopterygia.—The Ichthyosaurians are in some respects the most primitive of the Reptiles, and, both in the skull and vertebral column, show the characters of Labyrinthodonts. It is the single occipital condyle which marks the order as Reptilian, and in its large size and transversely rounded ball it makes a nearer approach to the condition seen in *Pareiasaurus* than does any other Reptile. In the post-orbital region of the head the arrangement of the bones in *Ichthyosaurus* is entirely Labyrinthodont. Behind the eye the post-orbital bone is exceptionally strongly developed, and between the squamosal and quadrato-jugal bones the supra-temporal is also preserved, and combines with them to cover the quadrate bone, so that in these respects the Labyrinthodont characters are quite as strong in *Ichthyosaurus* as in *Pareiasaurus,* and the only features in which the skull of *Ichthyosaurus* is less Labyrinthodont are the presence of a lachrymal bone (which is not perforated by a lachrymal canal as in *Ptychognathus*), in the absence of the so-called epiotic plates from behind the squamosal bones, and the absence of the mucus-canals between the orbits and nares. And thus it holds an intermediate position, so far as the preservation of those osteological conditions is concerned, between *Pareiasaurus* and ordinary Reptiles. And, since the supra-temporal bone covers the auditory region of the head, it is manifestly a bone which, with advantage to the animal, may be replaced by a membrane in terrestrial and littoral animals.

In the shortness of its vertebræ and absence of the transverse expansion of the neural arch, no less than in the mode of attachment of the ribs, *Ichthyosaurus* is totally unlike *Pareiasaurus.* But its vertebral characters are in many respects Labyrinthodont. The deep biconcave form of the centrum is paralleled in *Eosaurus,* and in other genera the centrum is equally short. The neural arch is not unlike that of *Mastodonsaurus,* and the ribs are similar in *Anthracosaurus* and other genera. The mode of their attachment is distinctive, but may be correlated with oceanic habits, since *Pareiasaurus* has both attachments for cervical ribs on the centrum, and *Ichthyosaurus* preserves the double-headed attachment in all presacral vertebræ.

The Oxford Clay genus *Ophthalmosaurus* has the clavicles more expanded than other Ichthyosaurs, and the clavicles embrace the inter-clavicle by a mode of union which is like that seen in *Pareiasaurus;* but the resemblance of the clavicular arch, like that of the vertebral column, is much less obvious with *Ichthyosaurus* than with Nothosaurs.

Resemblances to the Nothosauria.—The skeletons of the Nothosaurians are imperfectly preserved, but, although the skull is typically Reptilian, as showing no traces of Labyrinthodont structures, the remainder of the bones have preserved evidences of their origin from an Amphibian ancestor, which are well marked in both the vertebral column and the limbs The large transversely expanded neural arch, the elevation of the ribs to the neural arch in the dorsal region, the structure of the shoulder-girdle and pelvic bones and limbs, are all strongly Labyrinthodont. And, the group is represented in South Africa, in rocks apparently of the same age as those which yield the *Pareiasaurus,* by species of the genus *Mesosaurus.* All the long bones of the Nothosauria and Plesiosauria ossify in the same way as the long bones of living Frogs, and consist of cylindrical girdles into which long conical epiphyses penetrate, so as to meet, or nearly meet, in the middle of the shaft, from which they are often easily or naturally separated. I have had no opportunity of determining whether this condition is present in the long bones of Labyrinthodonts, and I only otherwise know it as a rare condition in some of the long bones of Chelonia from the Cambridge Greensand, and in an undescribed epiphysis, which I believe to be Dinosaurian, from the Oxford Clay, and in the proximal end of the tibia of *Protorosaurus.* A section of a vertebra of *Nothosaurus* shows that the centrum has ossified in the same way, as a periosteal sheath, and by conversion of the notochordal substance into bone at both ends. In *Mesosaurus,* and its South American representative named *Stereosternum,* a tubular notochordal canal remains at each end of the centrum like that figured in the vertebræ which were originally referred to *Pareiasaurus.* Although the mode of articulation of the ribs in Mesosaurs is different, and the form of the neural arch is not the same, there is enough in common to make the correspondence in the clavicular arch important as a mark of affinity, for in no other group have the bones either similar forms or arrangement. The resemblance is closer with *Nothosaurus* than with any of the smaller types. *Labyrinthodon rutimeyeri* * demonstrates the resemblances of the limbs, and pelvic and shoulder-girdle bones, with these Nothosaurs in a striking way, and the femur and smaller limb-bones of *Mastodonsaurus* are essentially of the same forms as in *Nothosaurus, Neusticosaurus,* and *Pachypleura.* The ilium is essentially like a diminutive ilium of a Teleosaur, which is not altogether incomparable with some forms of the bone in Crocodiles and in Theriodonts. Hence I would urge that, if Nothosaurs, and their marine representatives, the Plesiosaurs, have ceased to be Labyrinthodont in their skulls, the original characters have been retained in a remarkable way in the skeleton, which, in the vertebral column, and especially in the double attachment of the cervical ribs of Plesiosaurian genera, offers instructive collateral evidence of the nature of similar conditions in *Pareiasaurus.*

Resemblances to Ornithosauria.—Even in this highly modified group of animals instructive resemblances in the pelvis are detected with primitive types like the Protorosauria and Anomodontia, which indicate a common origin. And, if the forms of the pelvic bones in *Rhamphorhynchus, Cycnorhamphus, Phocosaurus,* and *Platypodosaurus* are compared, the conclusion follows that the pelvic bones in these widely divergent groups—like the sacrum—are similar in plan, and this similarity is not without its suggestive side as to the relation of the more highly differentiated types of Reptiles and Birds to the groups which are but little modified from the Labyrinthodont condition.

Resemblances to Crocodilia.—The upper surface of the skull of an Alligator or Crocodile is perhaps more like the skull of a Labyrinthodont than is that of any other existing Reptile. The positions of the vacuities in the head, the small size of the premaxillary bones, no less than the external sculpture, make it suggestively comparable. But in the post-orbital region there is a vacuity which in the living animals is closed with a stout membrane. That membrane occupies the positions of the post-orbital and supra-temporal bones, so that if it were ossified a bone would stretch from the squamosal to the quadrate, and completely cover the quadrate, as in Labyrinthodonts and Ichthyosaurs, and a bone would border the back of the orbit and stretch from the post-frontal to the jugal in the position of the Labyrinthodont post-orbital. Hence I suggest that, although these bones have ceased to be ossified, the preservation of a membranous representative in the Crocodilian skull is strong evidence of the mode by which the Labyrinthodont skull lost its external characteristics and became Crocodilian. It therefore furnishes evidence of some importance as to the nature of the relation between the skulls of *Pareiasaurus* and ordinary Anomodonts. We should search in vain for any condition which so nearly approximates to the mode of attachment of the ribs in Labyrinthodonts and *Pareiasaurus* as is seen among Crocodiles, especially in their early dorsal vertebræ, in which the head of the Crocodilian rib is inferior in position to the tubercle. There is no doubt that in most vertebral characters the *Pareiasaurus* is intermediate between Crocodiles and Nothosaurs.

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* WIEDERSHEIM: 'Schweizer. Paläont. Gesell.,' vol. 5, 1878.

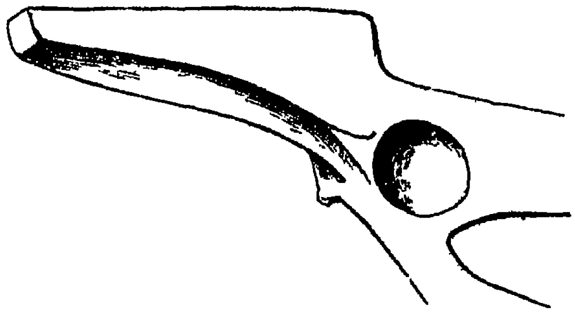
Hence, without examining the Amphibian characters of Dinosaurs and Birds, on which Crocodilian structures throw much light, it may be affirmed that there is conclusive evidence that many orders of true Reptiles preserve Labyrinthodont characters in their skeletons which are comparable to the characters of *Pareiasaurus*, so that, though *Pareiasaurus* is more Labyrinthodont than other Reptiles, it is only in the sense of showing for the first time Labyrinthodont characters in some parts of the skeleton in which they had not previously been observed, just as other Reptiles had previously shown Labyrinthodont characters in different parts of the skeleton; and on that account the characters of *Pareiasaurus* may not imply nearer affinity with Labyrinthodonts than is shown by Ichthyosaurs, Nothosaurs, and Crocodiles. On this evidence I am constrained to recognize the preponderating evidence of affinity with the Anomodontia and Theriodontia, and regard *Pareiasaurus* as the type of a sub-order, the Pareiasauria, which may probably be included in the Anomodontia.

The Mammalian Characters of Pareiasaurus.

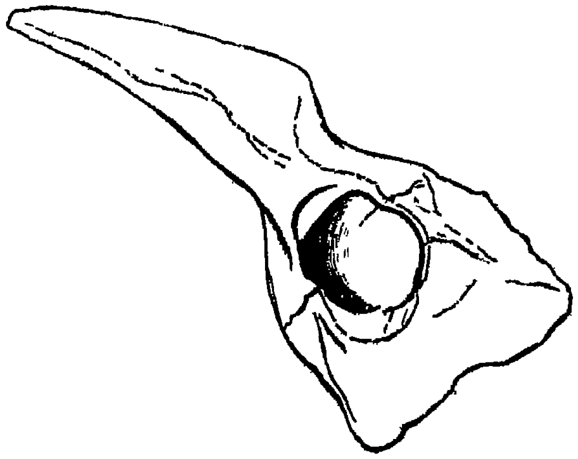
Resemblances to the Mammalia in certain of the South African Reptilia have been pointed out by Sir R. OWEN in the general character of the Theriodont skulls, in their dentition, in the sacrum, pelvis, and certain of the limb-bones. Similar conclusions have been urged by Professor COPE on the evidence of many remains of allied animals found in the Permian rocks of the United States, which he refers to a group named Theromorpha. The resemblance to a Mammal in the pelvis referred to *Dicynodon* is quite as marked as in that which has been named *Platypodosaurus*; and in this respect *Pareiasaurus* is strictly comparable with them. Many isolated bones of different generic forms show that these characters are not accidental characteristics, but pervade all the known representatives of the Anomodont group. The significance of these resemblances seems to me to admit of exactly the same kind of

DIAGRAM OF MAMMALIAN PELVIC CHARACTERS OF THE ANOMODONTIA.

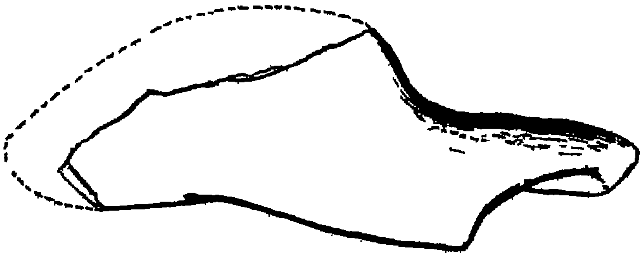
Marsupial or Dicynodont *type, with a small sacrum.*



Ilium of *Macropus*

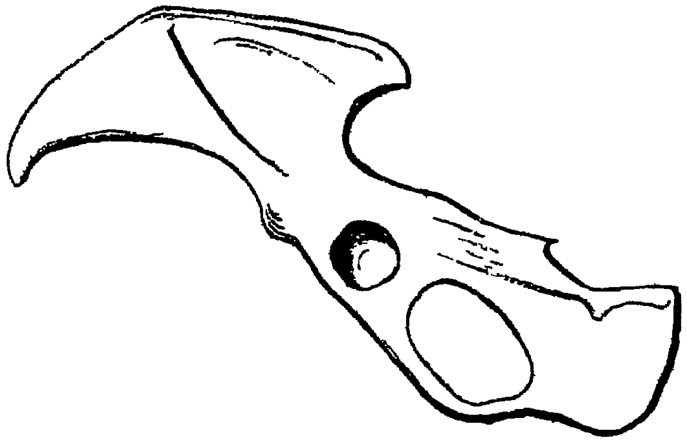


Pelvis of *Dicynodon tigriceps.*

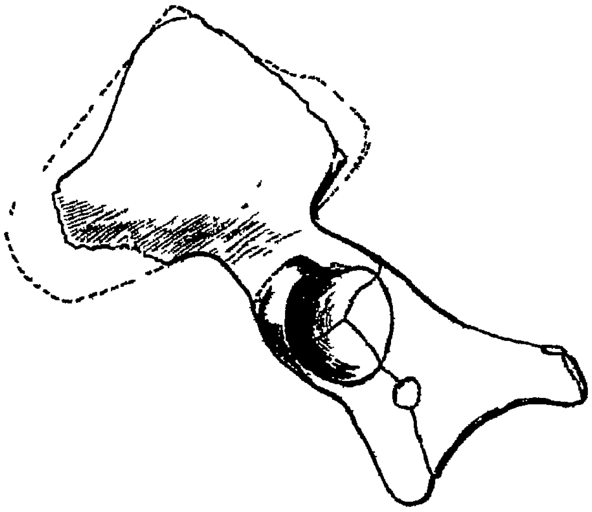


Ilium of *Pareiasaurus bombidens*

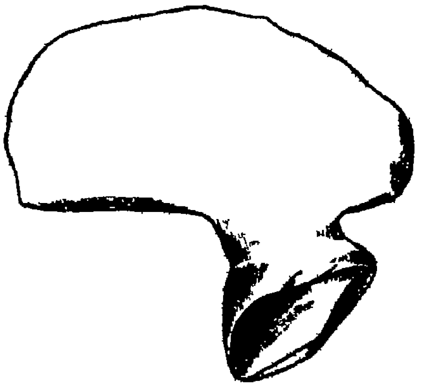
Edentate or Theriodont *type, with a longer sacrum*



Pelvis of *Orycteropus.*



Platypodosaurus robustus.



Ilium of Anomodont.

demonstration as the Labyrinthodont characters of *Pareiasaurus;* and I would urge that, just as we are entitled to infer from the presence in that Reptilian genus of Labyrinthodont structures that the characters have been inherited, so we are led to conclude from the presence of Mammalian characteristics in that and allied genera that the Mammalian structures have been transmitted to Mammals, if not in a direct line, which is improbable, by collateral derivation from a common ancestry. The evidence in this argument is very similar to that which led to the recognition of the

Avian affinities of certain Dinosaurs, and is about as complete as that evidence was when the conclusion was first enunciated by Professor HUXLEY. If it is legitimate to infer from certain characters of the pelvis and hind-limb of *Iguanodon*, combined with less marked resemblances to Birds in certain vertebral and cranial characters, that the Dinosauria and Birds are parallel offshoots from a common stock, then it must similarly follow, from the correspondence with the Mammalia shown by *Pareiasaurus* and its allies, that those groups also are parallel offshoots from a common ancestral type. The interest of this conclusion appears to be augmented by the fact that reasons have already been adduced for believing that most, if not all, of the Reptilian orders have an inheritance of Labyrinthodont characters, and are therefore derived from Amphibia; so that the Mammalia and Reptilia would thus appear to have a common origin, to which *Pareiasaurus* approaches nearer than any animal hitherto known.

EXPLANATION OF PLATES 12 TO 21

PLATE 12.—*The Skeleton.*

Fig. 1. Dorsal aspect of *Pareiasaurus bombidens*, showing the entire skeleton.
,, 2. Ventral aspect of the same animal.
(One quarter natural size.)

s. skull. *m.* mandible. *sc.* scapula. *ic.* inter-clavicle. *cl.* clavicle. *sr.* pre-coracoid. *n.s.* neural spine. *par.* parapophysis. *in.c.* inter-centrum. *r.* dorsal rib. *d.* diapophysis. *sm.* sacrum. *sr.* sacral rib. *i.* ilium. *a.* articular surface. *p.a.* pubic suture. *is.a.* ischiac suture.

PLATES 13–16.—*The Skull.*

Plate 13. Dorsal aspect of skull of *Pareiasaurus bombidens* (OWEN)
(One half natural size)
Plate 14. fig. 1. Anterior aspect of the same skull.
,, 2. Left side of skull, with sutures from the right side.
(One half natural size.)
Plate 15. fig. 1. Palatal aspect of the same skull, one half natural size.
,, 2. Outline of section of pterygoid bones in the type skull, of the natural size.
Plate 16. fig. 1. Palatal aspect of skull of *Pareiasaurus serridens* (OWEN), one half natural size.
,, 2. Section of tooth in the lower jaw of the same species, natural size.

pm. pre-maxillary bones. *in.* infra-narial bone. *m.* maxillary. *mr.* malar.

qj. quadrato-jugal. *sq.* squamosal. *st.* supra-temporal. *pt f.* post-frontal. *po.* post-orbital. *pf.* pre-frontal. *n.* nasal. *f.* frontal. *p* parietal ? *so.* supra-occipital. *e.* ? epiotic. *bo.* basi-occipital. *bs.* basi-sphenoid. *pt.* pterygoid. *pt.r.* pterygoid ridges. *m.d.* dentary bone. *m.s.* mandibular suture. *d.* teeth. *x.* position of attachment of lower jaw to skull. *v.* palatal vacuities.

PLATES 17–19.—*Vertebral Column.*

Plate 17. Restorations of the natural size, partly based on measurements.
fig. 1. Left side of a cervical vertebra.
„ 2. Posterior aspect of a cervical vertebra.
„ 3. Cervical rib.
Plate 18. fig. 1. Anterior aspect of a dorsal vertebra. } These figures are one half
„ 2. Right side of a dorsal vertebra. } natural size.
„ 3. Left side of a caudal vertebra. } These figures are of the
„ 4. Anterior aspect of a caudal vertebra. } natural size.
„ 5. Pelvis of *Rhamphorhynchus.*
„ 6. Pelvis of *Dimorphodon.*
Plate 19. fig. 1. Anterior aspect of pelvis, sacral rib, and ilium in natural position. (One half natural size.)
„ 2. External view of ilium. (One third natural size.)

pz. pre-zygapophysis. *ptz.* post-zygapophysis. *d.* diapophysis *p.* parapophysis. *t.* transverse process. *i.c.* sub-vertebral wedge bone or intercentrum. *n.s.* neural spine. *s.r.* sacral rib. *i.* ilium. *n.c.* neural canal.

PLATE 20.—*Shoulder Girdle.*

Fig. 1. Left side of clavicular arch seen from above.
„ 2. Lateral aspect of left side of clavicular arch, and scapular arch.
„ 3. Section showing the relations of the clavicle and inter-clavicle.

ic. inter-clavicle. *c.* clavicle. *s.c.* scapula showing *g.* articular surface, with pre-coracoid in front, pierced by foramen.

PLATE 21.—*Pelvis.*

Fig. 1. Pelvis of *Phocosaurus*, five-twelfths natural size.
„ 2. Diagram showing anterior aspect of the pelvis restored.
„ 3. Outline of pelvic bones of *Phoca vitulina.*

i. ilium. *p.* pubis. *p.p.* pre-pubic process. *f.* obturator foramen. *isc.* ischium. *su.* ischio-pubic suture. *a.* articulation.

IV. *The Development of the Branchial Arterial Arches in Birds, with special reference to the Origin of the Subclavians and Carotids.*

By JOHN YULE MACKAY, *M.D., Senior Demonstrator of Anatomy, Glasgow University.*

Communicated by Professor CLELAND, *M.D., F.R.S.*

Received May 29,—Read June 16, 1887.

[PLATES 22—25.]

THE manner in which the large arteries springing from the aorta in the higher Vertebrates have been developed from a set of arches comparable to the branchial vessels of Fishes has been clearly explained by RATHKE,* and since his time the views which he first set forward in the year 1857 have been almost universally accepted and taught. I have been led to believe, however, from the observation of certain facts in the anatomy and development of Birds, that the deductions which RATHKE made, drawn chiefly from his studies in Mammalian and Reptilian embryology, are not applicable to this class in so far as concerns the origin of the carotid and subclavian arteries. I am inclined to think also that the theories now generally held will be found inadequate to explain the origin of these vessels in the case of Chelonian and Crocodilian Reptiles, and to a less extent probably in Mammals.

ANATOMY OF THE LARGER ARTERIES IN BIRDS.

The aorta, arising from the left ventricle of the heart, passes at first forwards, upwards, and to the right side; then, changing its direction, it arches over the right auricle, and, sweeping backwards dorsal to the root of the right lung, gains the middle line. In the first part of its course two large vessels, the brachio-cephalic or innominate trunks, are given off.

The innominate arteries arise in close proximity to one another. They usually give no lateral branches, but terminate by dividing into carotid and subclavian vessels. Occasionally, however, a small branch is supplied to the front of the trachea, but this is more frequently an offset from the subclavian or carotid.

The common carotid arteries, passing forwards from their origin, bend round the œsophagus to reach its dorsal aspect, and, there approaching one another, gain the middle line, and are continued forwards towards the head in the canal formed by the

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* H. RATHKE, "Untersuchungen über die Aortenwurzeln und die von ihnen ausgehenden Arterien der Saurier." 'Wien, Akad. Denkschr.,' vol. 13, 1857 (*Abth.* 2), pp. 51—142.

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inferior spinous processes. Emerging from this canal opposite the third or fourth cervical vertebra, the vessels separate from one another, and, passing still further onwards, break up into numerous branches. The vessels of the right and left sides are often symmetrical in size and position, but one or other is sometimes of less diameter than its neighbour. In many cases one vessel is wanting altogether (all Passeres, GARROD*).

Fig 1.

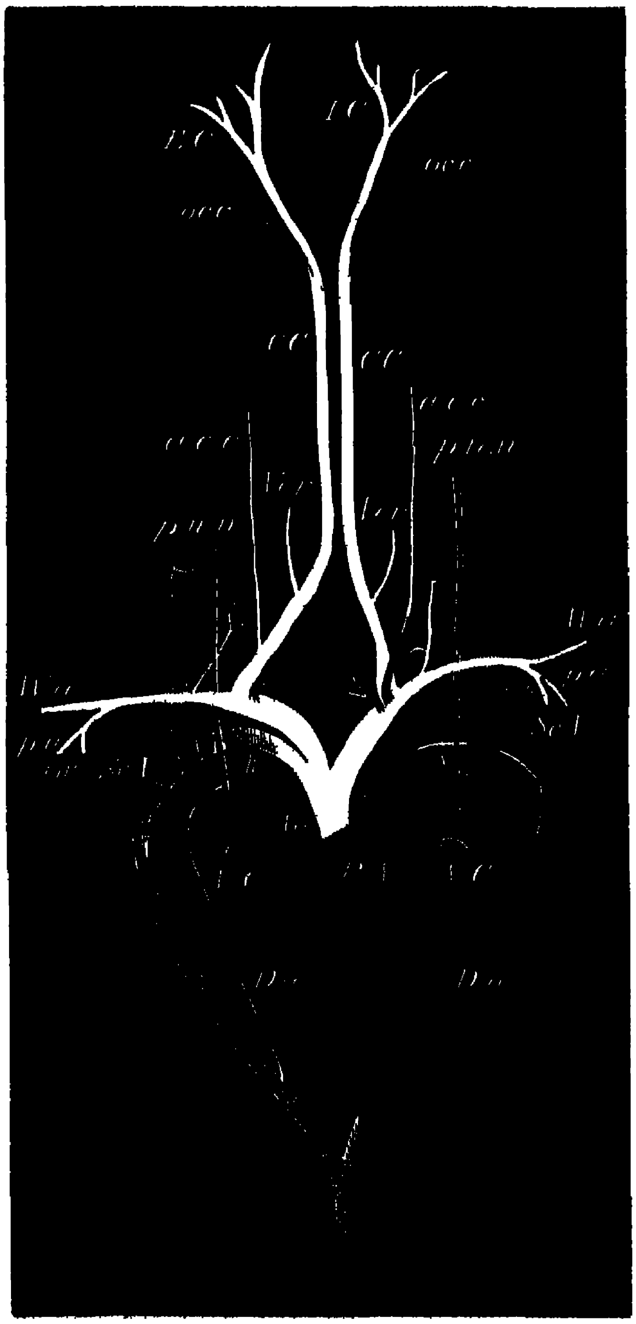

Diagram of the Arterial System of the Bird.

a, aorta; *I*, innominate; *C.C.*, common carotid; *E C.*, external carotid branches, *I C*, internal carotid branches; *occ.*, occipital; *Ver.*, vertebral; *a.c.c.*, arteria collateralis colli; *W.a.*, wing artery; *p.a.*, pectoral artery; *i.m.*, internal mammary; *Sc.V.*, subclavian vein; *V.C*, vena cava; *p.n.*, pneumogastric nerve; *P.A.*, pulmonary artery; *D.a.*, ductus arteriosus.

In the Ground Hornbill (*Bucorvus abyssinicus*) the arteries, passing forwards to supply the head, run in the lateral parts of the neck, and are not to be compared to the carotids of other Birds; but OTTLEY* has pointed out that two obliterated cords, representing the right and left carotids respectively, are to be found in the usual situation. In some Parrots the carotid artery of the right side runs forward in the usual manner, while the left vessel passes along the lateral aspect of the neck, as in the Ground Hornbill (GARROD).

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* GARROD, "On the Carotid Arteries of Birds," 'Zool. Soc. Proc.,' 1873, pp. 457–472; also 'Collected Papers,' London, 1881.

The branches of the common carotid are numerous · (1) a small branch running upon the front of the trachea, often, however, derived from the subclavian or innominate, (2) branches rising along with No. 1, supplying the lateral parts of the neck, and anastomosing in front with maxillary branches; (3) the vertebral, which after giving a branch to the muscles around the scapula enters the foramen in the transverse process of the second lowest cervical vertebra, and there splits into two divisions, the anterior and larger passing onwards towards the head to anastomose with the occipital artery, the posterior running backwards to the thorax, supplying one or two intercostal spaces; (4) a number of very slender branches are given off to the muscles upon the front of the vertebral column—these correspond in position to the interspaces between the cervical vertebræ; (5) the occipital artery, running in a dorsal direction to anastomose behind the skull with the vertebral artery; (6) a vessel called internal carotid, which, however, distributes a number of branches to the external aspect of the cranium, and to the anastomosis at the back of the orbit, before entering the cavity to supply the brain; (7) the external carotid, so-called, the main artery of the external aspect of the head, dividing into branches named by OWEN† "external maxillary," "laryngeal," "lingual," "hyoid," and "internal maxillary"; from one of the branches or from the main trunk twigs pass backwards in the neck to anastomose with set No 2. It is important to notice that there is no clear subdivision into branches corresponding to external and internal carotids as in Mammals, but that vessels belonging to the right and left sides, whose destination is the anterior end of the trunk, run forwards underneath the vertebral bodies in the same manner as the aorta passes backwards.

The subclavian arteries, from the extremities of the innominate stems, cross outwards to the anterior limbs. The largest branch is distributed to the pectoral muscles, but, in addition, the internal mammary artery is given backwards, and in many cases a vessel is directed forwards to the ventral aspect of the trachea, and to the skin upon the under-surface of the neck. No intercostal arteries are supplied. The subclavian arteries are distinguished by this important fact, that in their course outwards they pass ventral to the pneumogastric nerves and to the superior venæ cavæ. In this they differ very markedly from the vessels which in Mammals and Lacertilian Reptiles supply the upper limbs, for these, after the manner of intercostal trunks, stretch outwards in a position dorsal to both vein and pneumogastric nerve. In Crocodilian and Chelonian Reptiles the relation of parts is similar to that found in Birds.

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[*] OTTLEY, "The Vessels of the Neck and Head in the Ground Hornbill," 'Zool. Soc. Proc.,' 1879, pp. 461–467.

[†] OWEN, 'Anatomy of Vertebrates,' London, 1866.

These facts, although probably widely known, do not seem to have been appreciated in their relation to the question of the development of the vessels, inasmuch as it is improbable that an artery running ventral to the vein and nerve, as does the subclavian in Birds, can correspond in origin with a trunk which, as in Mammals, crosses dorsal to these two structures Only two observers, so far as I have been able to ascertain, have taken notice of the different positions of the vessels. One of these, SABATIER,* has been led to propose a scheme of development differing in some respects from that of RATHKE, while the other, BRENNER,† in a paper on vascular abnormalities, merely notices the facts, and expresses a doubt as to the correctness of the accepted beliefs.

The intercostal arteries are directed chiefly from the aorta, but the first two or three spring from the vertebral.

Vestigial structures.—The right and left pulmonary arteries are each connected to the descending aorta by a ductus arteriosus round which the pneumogastric nerve sends it recurrent branch. These may be looked upon as completing the pulmonary arches. The left ductus arteriosus, passing dorsal to the root of the lung, is a long ligamentous cord which unites with the aorta usually opposite the sixth dorsal vertebra. The right one is described as a short structure passing into the posterior border of the arched portion of the aorta, but I have always found it, in my dissections, of considerable length, terminating in the descending aorta about half the breadth of a vertebra nearer the head than the place of termination of its neighbour of the left side.

Fig. 1, Plate 22, shows the ductus arteriosi of the Nandu (*Rhea americana*).

A vestige of the fourth left arch is present in a few Birds. I have not been fortunate enough to obtain for dissection any of the species in which this structure is found, but Professor A. MACALISTER, of Cambridge, has kindly furnished me with particulars from his own dissections. He has found it as a well-marked cord in the Osprey (*Pandion haliaetus*) and White-tailed Eagle (*Haliaetus albicilla*), and some other Raptores. He has also noticed it, but less distinctly, in some of the larger Gulls, especially in *Lestris pomarinus* and *Larus marinus.* When present it stretches from the innominate artery to the aorta as a ligamentous cord. This fact agrees very closely with what I have observed to be the method of its disappearance, described later.

SCHEME OF DEVELOPMENT ACCORDING TO RATHKE.

General accounts of the development of the arterial system in Birds will be found in all works upon Embryology, but the best and most detailed is probably that of FOSTER and BALFOUR.‡ Fig. 2, copied from RATHKE,§ explains the general system.

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* SABATIER, 'Études de Circulation Générale,' Montpellier, 1873; and 'Annales des Sciences Naturelles,' 1874.

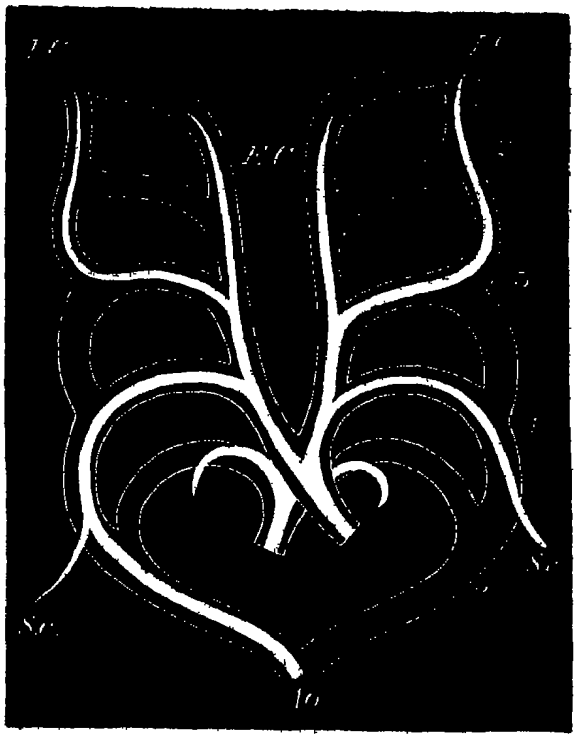
† BRENNER, "Ueber die Verhältnisse des Nervus laryngeus inferior Vagi zu einigen Aortenvarietäten des Menschen, &c.," 'Archiv Anat. Physiol. (*Anat. Abth.*),' 1883.

‡ FOSTER and BALFOUR, 'The Elements of Embryology,' 2nd edit, London, 1883.

§ *Loc. cit.*, Plate 6, fig. 9.

The fifth fœtal arches become the pulmonary arteries of the adult Bird, and each is completed by its ductus arteriosus

Fig 2.



Arches of the Bird (Rathke).

1, 2, 3, 4, 5, branchial arterial arches; *Ao.*, aorta; *S.c.*, subclavian; *E.C.*, external carotid; *I.C.*, internal carotid.

The fourth right arch becomes the aorta, while the dorsal portion of the fourth left disappears, except in those Birds in which it still persists as a solid cord. The subclavian arteries are regarded as lateral branches from the dorsal ends of the fourth or aortic arches, their adult position being reached subsequently by a supposed shortening of the arches from which they spring, by which their bases become fused with the carotid vessels to form the innominate arteries. The base of the left subclavian consequently represents the more ventral portion of the fourth left arch. The common carotids are regarded as the representatives of the vessels which in fœtal life connected, upon the ventral aspect of the alimentary canal, the fourth with the third arches. The external carotids are supposed to be the continuations of these vessels still further onwards in the direction of the second arch. The internal carotids are looked upon as the third arches, the posterior dorsal trunks, by which these should have been connected with the aortic arches, becoming obliterated and disappearing.

Fig. 3, "Diagram of the condition of the arches of the aorta towards the close of incubation," is copied from Foster and Balfour.* It represents a stage in the development in which the right subclavian artery is supposed to be found arising from the aortic arch, not yet having assumed its adult position. The left subclavian is pictured as being connected by a cord to the left ductus arteriosus, and dotted lines in front of the fourth arches stand for the already obliterated dorsal connections between the carotid and the aortic arches.

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* *Loc. cit.*, fig 93.

Fig. 3

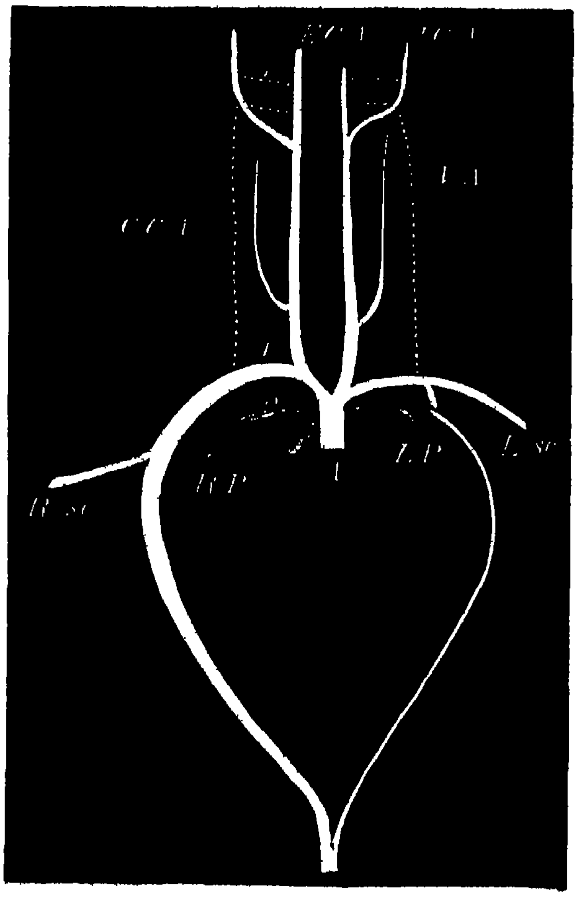

Diagram of the Condition of the Arches of the Aorta towards the close of Incubation. (Foster and Balfour).

1, 2, 3, 4, 5, the several aortic arches , *E C A.*, external carotid , *I.C.A.*, internal carotid ; *C C.A* , common carotid , *V.A* , vertebral , *R sc* , right subclavian , *L sc.*, left subclavian ; *R P.*, *L P* , right and left pulmonary arteries. The dotted lines show the portions of the arches which have been obliterated

I have examined embryo Chicks in nearly all the stages of their development, but have never seen the subclavian vessel arising from the arch of the aorta as depicted in fig. 3 ; indeed, it is impossible to conceive that if found in that position it could ever assume its adult relations to the pneumogastric nerve and superior vena cava. Even before the anterior limb has first made its appearance, the large vein of the neck may be seen crossing the ventral aspect of all the arches, and the identity of this vessel with the jugular vein of adult life is indisputable. The pneumogastric nerve is formed at a very early period, as is evidenced by the recurrent course, behind the fifth arch, of its laryngeal branch, which has been carried back by the descent of the arches from the neck into the thorax. If the subclavian artery passed to its adult position along the aortic arch, it would occupy a position dorsal to vein and nerve, instead of one ventral to both.

The scheme which Sabatier* has set forward to explain the origin of the subclavian vessels is shown in fig. 4. It will be noticed that the subclavians are represented as arising from the dorsal extremities of the third arches, the vessels which, according to RATHKE, become the internal carotids. To this, however, the same objections hold good, as the relations of the third arch to vein and nerve are similar to those of the fourth.

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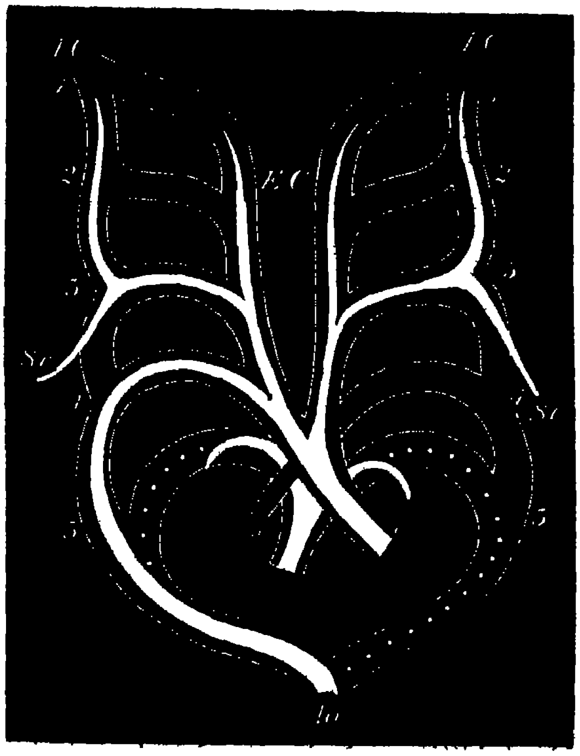
* Sabatier, *loc. cit.*

Fig 4.



Arches of the Bird (SABATIER).

1, 2, 3, 4, 5, branchial arterial arches; *Sc*, subclavian, *EC*, external carotid, *IC*, internal carotid; *Ao.*, Aorta.

Moreover, the common carotid arteries occupy a position dorsal to the œsophagus, and do so from a very early date; this is not what one would expect if they had originally occupied a ventral situation. From the observations detailed in the following pages I have been led to assign the origin of the subclavians to the ventral extremities of the third or carotid arches, and that of the common carotid stems to the third arches and the dorsal vessel above each, as is represented in fig. 2, Plate 22. Under this scheme the numerous branches of the common carotid are to be regarded in the same light as visceral and parietal branches of the aorta.

DEVELOPMENT OF THE SUBCLAVIAN AND CAROTID ARTERIES.

From the examination of a large number of Chick and Duck embryos I have become convinced that the theories now universally held are not in accordance with the facts of development. In relation to the subclavian arteries, the origin of which, as has been explained, RATHKE* assigns to the aortic roots, it ought to be possible to trace their gradual change of position, and to see the steps of the process by which they are supposed to pass from the dorsal to the ventral end of the arch, and finally to observe their gradual fusion with the bases of the carotid arteries to form the innominate trunks. It should be possible to describe in the history of their development distinct stages, in each successive one of which the subclavian arteries should be found springing from the aorta nearer and nearer to its ventral end, until the change is completed by their fusion with the common carotids. And, in addition, the method by which the arteries, arising at first dorsal to the pneumogastric nerves and jugular veins, become afterwards ventral to both should be capable of explanation. But this is not the case. The subclavian artery is to be observed first about the close of the third day of incubation, at a time when the pectoral limb has just begun to be discernible, and at its earliest appearance the artery is found arising from the third arch, not from the fourth. Moreover it springs from the ventral end of the arch, and stretches outwards in a plane superficial to, or ventral to, the pneumogastric nerve and jugular vein. It appears, therefore, first in what is practically its adult position, so that the innominate artery is not formed by the gradual fusion of the bases of subclavian and carotid, but is to be accounted for by the breaking up of the originally simple truncus arteriosus into canals continuous with each of the arches.

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* RATHKE, "Untersuchungen über die Aortenwurzeln, &c," pp. 79–81. In this passage, while RATHKE assigns the origin of the subclavian arteries of Birds to the dorsal ends of the fourth arches, he admits

According to RATHKE,* the common carotid with its branches representing the external carotid branches of the Mammal is the persistent ventral communicating vessel running from the fourth arch towards the head, while the internal carotid is the third arch, the dorsal communication between it and the fourth having disappeared. If this were true, then the subclavian, arising in the manner described above, should spring from the common carotid at the place of origin of its internal and external branches. But, in addition to this, it may be established by direct observation that at a period when the third arch is still dorsally connected with the fourth (during the sixth day) it is the common carotid artery, not the internal carotid alone, which is continued from the dorsal end of the arch to the head. The external carotid branches are not therefore the product of the ventral trunk, but are to be regarded simply as visceral and parietal branches of a dorsal vessel. The ventral trunk remains as a small branch from the subclavian or innominate arteries to the front of the trachea.

Description of Observations.

The earlier stages in the development of the arteries may be studied by the direct observation of the circulation in Duck or Chick embryos of from three to five or six

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that his direct observations upon their development do not satisfactorily prove this. His theory is founded upon the analogies between the development of Birds and Mammals, and he had already found in Sheep and Pig embryos that the subclavian arteries in these forms first appeared as branches from the original aortic roots. ("Ueber die Entwickelung der Arterien, welche bei den Saugethieren von dem Bogen des Aorta ausgehen," 'MÜLLER, Archiv Anat. Physiol.,' 1843, pp 276–302.)

* RATHKE, *loc. cit.*, pp. 75–78.

days In opening the shell, the vascular area of the yolk-sac is to be preserved intact The whole of the contents of the egg may be floated in water, and the embryo, together with the vascular area, after having been clipped from its connections, may be transferred to a slide and examined under the microscope. In Duck embryos of from three to five days the circulation may be easily observed under a low power with transmitted light, but in later stages a strong simple lens with reflected light will be found more convenient.

In Duck embryos, in the course of the fourth day, three arches may be seen: the first or mandibular, the second or hyoidean, and the third or carotid. In the earlier stages of this day the first is usually the largest, and is placed almost directly in a line with the truncus arteriosus, but in the later stages the second arch has increased in size relatively to the mandibular, and receives the direct flow of blood from the vessel springing out of the ventricle. The blood from the arches flows towards the anterior and posterior extremities of the embryo in a dorsal vessel, and there is no trace of a branch from the ventral extremity of the first arch. At the close of the fourth day I have been able to observe distinctly only two arches, the second and third, but it is to be noted that the tissue of the mandibular bar has by this time increased in density, and may possibly obscure a slender vessel. The pectoral limb forms but an indistinct projection on the lateral wall of the embryo, and no vessel can be seen running into it.

At the close of the fifth day three arches are distinctly to be seen: the third or carotid, the fourth or aortic, and the fifth or pulmonary. The first and second of these are nearly of equal size, while the third is much smaller. The ventral ends of the arches are all in close contact with one another, each division of the truncus arteriosus breaking up into the three vessels simultaneously. As they pass round the throat, however, the arches separate, and finally terminate at some little distance from one another in a continuous longitudinal vessel, the posterior portion of which, carrying blood towards the tail, is the aorta, while the anterior portion, in which the current is directed forwards towards the head, may be termed carotid. The vessel which passes forwards from the ventral extremity of the arches towards the head is small, and cannot be traced for any distance. On the other hand, I have seen in all my specimens a hitherto undescribed branch taking its origin from the anterior border of each division of the truncus arteriosus where it is passing into the carotid arch. This vessel, which afterwards becomes the subclavian artery, S in fig. 4 (Plate 22), runs backwards and dorsalwards for some distance along the ventral ends of the arches, and is lost upon the side of the neck near the spot where the superior cardinal vein passes into the ductus Cuvieri. The heart is still considerably in front of the limb, which at this date forms a distinct projection on the side of the embryo. No arterial vessel can be traced into the limb, nor are any of the intercostal branches of the aorta in the vicinity larger than the others The aorta gives off a number of lateral branches (intervertebral) in front of the anterior limbs, and, as these are not found in the adult, it is probable that they have disappeared during the descent of the heart and arches from the neck into the thorax; but, on the other hand, during the process the ventral vessel which I have described would be placed, on account of its posterior direction, in circumstances exceptionally favourable to development.

In the Chick during the fourth day a vessel similar to that which has been described in the Duck may be seen (Plate 22, fig. 4). About the beginning of the fifth day I have been able to trace it to the limb. At this date it is not apparent at first sight, as it is hidden to a great extent by the projecting portion of the auricle, but it may be demonstrated in the following manner. After the embryo has been rapidly and carefully removed from the egg in the manner already described, the amnion is to be ruptured and pulled aside. If, then, the neck be straightened by pushing the head forwards, the artery may be seen arising from the anterior border of the right or left division of the truncus arteriosus, at the spot where the arches are being given off. By depressing the prominent part of the auricle the vessel may be followed by the eye as it passes backwards. It passes first the ventral ends of the arches, and at the lower border of the fifth or pulmonary a lateral branch coursing in a direction dorsal and slightly towards the head is given off to the superficial parts of the neck. Behind this the vessel may be seen to cross the ductus Cuvieri, and still further backwards it may be traced to the base of the limb, getting deeper as it approaches its destination. If, now, the projecting portion of the hyoidean bar be pushed aside, a slender branch will be seen to be directed forwards upon the ventral aspect of the throat, arising from the base of the vessel just described. This small vessel can be followed but for a short distance. It is the only ventral prolongation forwards from the carotid arch. On the other hand, the vessel reaching towards the head from the dorsal end of the arch is large and prominent.

It is to be noted, therefore, from the direct observation of the growth of the blood-vessels in the living Chick, that no branch from the aortic root, the place of origin which RATHKE assigns to the subclavian, can be traced into the limb; but, on the other hand, an artery can be seen springing from the ventral end of the third arch, and may be traced on the fourth or fifth day to the limb. Further, the vessel on the ventral aspect of the throat, which RATHKE supposed became the external carotid branches of the common carotid stem, is seen to be of small size compared with the dorsal vessel, and to be connected at its base with the subclavian artery.

The presence of an artery running towards the limb from the ventral end of the third arch, and the relations of the dorsal carotid to the supply of the head, may be confirmed by sections of hardened embryos. But it is to be noticed that, owing to the oblique course of the subclavian artery, it is impossible to trace its entire length in one series of sections. Plates 22 and 23, figs. 5–10, represent a series of transverse sections through the anterior portion of the body of a Chick embryo about the close of the third day. The first of the series, fig. 5, is carried across the head slightly obliquely at the anterior end of the alimentary canal. Beneath the base of the brain the extremity of the notochord is seen, and immediately beneath that the carotid arteries, which here, for the first time in this stage of development, come into contact with one another. The anterior cardinal veins lie in the lateral aspects of the section. The succeeding figures represent sections taken at intervals from the series passing backwards towards the heart The carotid arteries may be traced backwards to the right and left aortic roots, their direct continuity with these being clearly demonstrated

No other arterial vessel is to be seen ventral to the throat or in any other part of the section until the heart is reached The first indication of any other artery in the neck is seen in fig. 7, the fourteenth of the series immediately above the level of the truncus arteriosus, where the ventral carotid is seen of exceedingly minute size The sections posterior to this show vessels running backwards, behind and external to the pericardium, in the position of the ventral subclavian already described in the living specimen.

Plate 23, figs 11 to 14, represents longitudinal antero-posterior sections through a Chick embryo at the close of the fourth day The first two, figs. 11 and 12, are carried through the right side of the body, the second two, figs 13 and 14, through the left side. They show the carotid and subclavian arteries in their relations to other parts In the first section, fig 11, the arterial arches are cut across close to their origin from the truncus arteriosus. The section is a little deeper in front than behind, and the alimentary canal and the superior cardinal vein are both to be seen in the anterior portion, while behind they are lost, to become visible, however, in the succeeding sections. Ventral to the extremities of the arches a vessel is seen running backwards and outwards, breaking up into two at the level of the most posterior arch. By comparing this section with the one immediately following it this vessel is seen to be on a plane superficial to the anterior cardinal vein. Of the sections through the left side, fig. 13 is the more superficial, and by comparing it with fig 14, the deeper one, the same relations are established The dorsal branch of the artery is more distinctly evident, and is seen to break up into secondary branches in the superficial parts of the neck.*

In the two deeper of the four sections the carotid arteries are represented passing forwards dorsal to the alimentary canal, and they are evidently continuous with the dorsal ends of the arches In these sections I was not able to find any ventral carotid vessel, so that it is probable that if such is present its size must be small compared to that of the other arteries figured. Figs. 15, 16, show the arches of a Chick embryo at the close of the fourth day, and demonstrate the continuity of the great carotid artery at this date with the dorsal end of the arches Fig. 15 shows the aorta, the dorsal ends of the three arches in close proximity, and the carotid arteries, fig 16, the section immediately following, represents the terminations of the three arches in the aortic roots.

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* HIS, in his work, 'Die erste Entwickelung des Huhnchens im Ei,' Leipzig, 1868, figures on Plate XI., figs 6 and 8, blood-vessels running in the body wall, in the position of the artery marked *s* in figs 5–14 described above In the description of his plates HIS does not take notice of these vessels, but they have the appearance of being continuous with the vessels which, in the succeeding fig. 9, he represents in the fore-limb

In another work, 'Anatomie menschlicher Embryonen' (Heft I.: Embryonen des ersten Monats), HIS describes and figures an artery arising from the ventral end of the fourth arch. Of this vessel he says, at page 79, "Von dem Anfangsstucke des vierten Bogens geht ein Aestchen in die Rumpfwand. Der Gedanke, dass es der Anfang einer Arteria subclavia sein mochte, lässt sich deshalb nicht festhalten, weil dies Gefäss nach RATHKE's Beobachtungen aus dem Endstücke des vierten Aortenbogens entsteht."
—[September 21, 1887]

The carotid arteries, prolonged through the neck from the dorsal ends of the arches, do not at first occupy the middle line, like the aorta in its backward course, but run forwards, separated from one another by some distance, being nearer to one another in front and behind than in the middle portion of their course This may be seen by an examination of figs 5–10. RATHKE* has described the course of the carotid arteries in the neck of the Chick, and pointed out that they are at first placed at some distance from the middle line, and that it is not until the eleventh or twelfth day that they assume their median position. I have found in my dissections, however, the two arteries in close proximity on either side of the middle line during the seventh, and even at the close of the sixth, day. It is important to notice, however, that even when they are at some distance from one another they are the continuation of dorsal vessels, and are not ventral arteries which are passing upwards to assume a dorsal position, as RATHKE believed.

Figs. 17 to 26 are chosen at intervals from a series of vertical transverse sections of a Chick embryo at the close of the fifth day. They demonstrate the relations of the carotid arteries to the vascular arches at a later stage of development than the preceding series. They also show, along with the next series, the first stages in the disappearance of the fourth left arch. Fig. 17 shows a section through the cardiac end of the truncus arteriosus, and five canals are found, three lying to the right side and two to the left; but the more anterior of the two is large, and bears evidence of being made up of two canals, which are fusing with one another. This becomes more apparent in the next section, which follows in the actual series immediately upon its predecessor, the two portions of the anterior large canal being partially constricted off from one another. Fig. 19, which still shows the undivided truncus arteriosus, presents a section of six passages, the two portions of the originally large one being now distinctly separate. The next section, which is a little more dorsal than the last, shows the two divisions of the truncus arteriosus immediately ventral to the ends of the arches. This and the next figure show traces of lateral branches passing from the most anterior arch. Fig 22, at a short interval from the last, shows the arches as they are passing dorsalwards by the sides of the alimentary canal, and the superior cardinal veins on each side external to the arteries. In the anterior portion of the section the carotid arteries are shown cut across as they run forwards. The next four figures, which complete the series, represent the extremities of the arches, and they demonstrate the continuity of the carotids with the dorsal ends of the most anterior arches, and show that they occupy the same plane as the aortic roots. The three arches present on the fifth day are the third, fourth, and fifth; and it is important to notice at this date the proximity of their dorsal ends to one another, and the continuation forwards from the third of the great artery to the head.

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* RATHKE, "Ueber die Carotiden der Krokodile und der Vögel." 'MÜLLER, Archiv Anat. Physiol,' 1850, pp 184-192.

RATHKE, "Ueber das Verhalten der Carotidenstämme des Huhnes wahrend ihrer Entwickelung." 'MÜLLER, Archiv Anat Physiol,' 1852, pp. 372-374.

RATHKE, "Bemerkungen über die Entstehung der bei manchen Vögeln und den Krokodilen vorkommenden unpaarigen gemeinschaftlichen Carotis" 'MÜLLER, Archiv Anat Physiol.,' 1858, pp 315–322.

RATHKE, "Bemerkungen über die Entstehung der Carotis subvertebralis bei der Krahe" 'MÜLLER, Archiv Anat. Physiol.,' 1859, pp. 382–384.

On the fifth day the canal leading to the fourth left arch becomes fused with that leading to the third, but the arch is still of undiminished size in its course dorsalwards. The next series, figs. 27 to 30, show the arches of an embryo Chick about the beginning of the sixth day The fourth left arch is now reduced to a cord lying between the carotid and pulmonary vessels, and it may be traced dorsalwards to the extremity of the arches, where it probably joins the aortic root

These facts account for the presence in some of the Raptores of a solid cord stretching from the innominate artery to the aorta. In most Birds this cannot be found, and the fourth left arch has probably disappeared altogether. I am inclined to think, however, that in some cases the cord above described fuses with the coats of the pulmonary arch immediately behind it, as I have found in certain instances —notably in the Heron (*Ardea cinerea*), Solan Goose (*Sula alba*), and Swan (*Cygnus olor*)—a ligamentous band stretching from the base of the left innominate artery to the ventral surface of the left pulmonary vessel. In the series of sections the connection of the carotid artery with the dorsal end of the arches is still apparent.

In embryos at the close of the sixth day, and in older forms, the arrangement of the vessels may be investigated by dissection under water with the aid of a simple lens. If such a dissection be made at the close of the sixth day, there will be found three arches upon the right side, but only two upon the left. The subclavian arteries arise upon each side from the anterior border of each division of the truncus arteriosus, just beyond the pericardium. They pass outwards and backwards ventral to the pneumogastric nerve and the accompanying vein, and reach the limbs, in which they may be traced for some distance. Indistinct indications of branches may be noticed, but not so clearly as to admit of accurate description. The carotid artery is continued upwards from the dorsal end of the third arch upon each side, and is the only vessel which carries the blood supply to the head. The carotid arch upon each is connected dorsally to the arch behind it, namely, the fourth upon the right side and the fifth upon the left, the fourth left having disappeared. The dorsal connecting vessel is at this date slender, but it may always be demonstrated by careful dissection. In one instance, in which the injection of the blood-vessels was exceedingly successful, I noticed upon the right side a slender lateral branch given off from the connecting cord apparently to the muscles of the neck. This vessel, if its presence be constant, probably is the suprascapular artery, which, in adult life, arises either from the base of the carotid or from the vertebral. It is important to notice at the close of the sixth day that, while the third arch is still complete, the common carotid artery, the *only vessel which passes to the supply of the head*, is prolonged from the *dorsal extremity* of the arch, and occupies a position on the front of the ventral bodies close to the middle line and to its fellow of the opposite side. The subclavian artery is also found in what is practically its adult position. Fig 31 represents diagrammatically the arteries upon the right side at the close of the sixth day.*

The changes which take place in the later stages of incubation are easily followed. The heart passes still further back into the thorax, so that the subclavian arteries, which, upon the sixth day, were directed backwards a little, pass, upon the ninth day, almost directly outwards, and, at a period still later, will be found to stretch forwards a little. On the ninth day most of the adult branches may be dissected out; one small one from the base of the parent trunk, passing forwards and inwards to the front of the œsophagus and trachea, can be traced for a short distance, and seems to represent the ventral prolongation of the truncus arteriosus The connecting cord between the dorsal end of the third or carotid and the arch immediately succeeding it is lost about the close of the seventh day, and the space between the carotid artery and the aorta is slightly enlarged; but otherwise these two arches maintain their relative positions to one another. At this time, too, the common carotids may easily be followed forwards upon the dorsal aspect of the alimentary canal, and most of their branches may be made out,

Summary of the Embryology of the Carotid and Subclavian Arteries in the Bird.

After the disappearance of the first two arterial arches (mandibular and hyoidean), which takes place in the Chick on the third day, the three permanent arches become established. From the most anterior of these, the carotid arch, two vessels are prolonged forwards. One of these, from the ventral extremity of the arch, runs upon the under-surface of the alimentary canal, and is of small size It can be traced only for a short distance towards the head. It survives in the adult as a slender set of branches from the subclavian or from the base of the common carotid, directed to the ventral surface of the trachea and œsophagus and neighbouring parts. This is the vessel which RATHKE regarded as the common and external carotid. The other forward prolongation is from the dorsal end of the arch. It is large and always easily followed. It is at first in direct continuity, upon each side, with the aortic root, but afterwards this continuity is interfered with by the dwindling of that portion of the stem which lies between the extremities of the third and fourth arches. The connection is finally completely broken through by the end of the seventh day. RATHKE regarded this as the internal carotid, but it constitutes the sole blood-supply of the head, and becomes the common carotid of the adult Bird, which is thus the persistent third arch (see fig. 2, Plate 22) and its dorsal continuation forwards.

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* In a paper, "Entwickelung der Branchialbogen und Spalten des Hühnchens," in 'Archiv Anat Physiol. (*Anat. Abth.*),' 1887, Dr MALL, in the course of a research into the development of the thyroid and thymus glands, figures, in a Chick of the seventh day, the right subclavian artery as arising from the ventral end of the third arch, and passing in its course superficial to the jugular vein. Dr MALL does not, however, in his paper consider the question of the development of the blood-vessels. [Sept 21, 1887.]

Confirmation of the fact just stated with regard to the common carotid artery is found in a remarkable abnormality which I met with in the dissection of a Guillemot (*Uria troile*), and which is represented in Plate 25, fig. 32 The remains of the dorsal connection between the third and fourth arches upon the right side are present as a distinct cord passing between *the common carotid artery* and the descending portion of the aortic arch The cord is connected with the carotid artery immediately behind the origin of the vertebral branch. The other arteries were quite normal. The only interference with the usual arrangement which the presence of this cord entailed was that the carotid artery of the right side reached the dorsal aspect of the œsophagus a little earlier than its fellow of the left side

If RATHKE's theory be accepted, the presence of this cord remains unexplained. According to him, if the dorsal connection between the third and fourth arches were found persisting, it would stretch the whole length of the neck from the internal carotid artery at the base of the skull to the aorta in the thorax. I have found in the Crocodile (fig 33), upon both sides of the neck, cords similar to that described in the Guillemot, from the lower ends of the common carotids to the aortæ.

The subclavian artery at its earliest appearance is a branch derived from the ventral end of the third arch, and not from the aortic root as RATHKE has it. It is appreciable, at the end of the third day, as a vessel passing backwards in the ventro-lateral parts of the neck, and may be traced into the limb at the end of the fourth or in the earlier hours of the fifth day Its most important branch, upon the fourth and fifth days, is one to the superficial parts of the neck, and passes from the parent trunk in a dorsal direction. Its adult arrangement of branches is discernible on the ninth day.

The arches arise at first in close contact with one another on each side from the extremity of each division of the truncus arteriosus, and it is only when the parent vessel splits up into its component parts that the ventral ends of the arches are separated from one another. The innominate arteries, while theoretically expressing the ventral vessels uniting the third and fourth arches, are really portions of the truncus arteriosus. In the same way the first portion of the aorta and the first portions of both pulmonary arteries, as far outwards as the spots where the obliterated ducti arteriosi spring, are developments from the truncus arteriosus. The aortic arch was supposed by RATHKE* to have shortened considerably, in order to bring the subclavian from a position upon the root to the innominate stem. The improbability of this is shown by a comparison of Plate 22, fig. 1, and Plate 25, fig. 32, which represent the various obliterated cords attached to the aorta. Each of these maintains the relative position which in early fœtal life it occupies, and which a subsequent shortening of the large trunk would have altered.

COMPARATIVE ANATOMY OF THE CAROTID AND SUBCLAVIAN ARTERIES.

General Statement.

The examination of the comparative relations of the carotid and subclavian arteries in the different groups of Vertebrates throws additional light on the manner in which these vessels are developed in the Bird The chief difficulty is to be met with in connection with the nomenclature, and is to be accounted for by the fact that accurate comparisons between the arteries of different groups have not been made, observers having often named vessels from their position in one form without reference to their relations in others. This is particularly the case with reference to the carotid system.

The carotid system consists of the following parts:—(1) The third arch , (2) its dorsal prolongation towards the head; (3) its ventral prolongation towards the head. The last-named portion, the ventral prolongation towards the head, is, in the Amphibia, an artery supplying the ventral aspect of the neck, extending as far as the tongue, to which it distributes branches. It has been named variously "lingual artery" and "external carotid artery," but, if the name carotid be applied to it at all, it were better called "ventral carotid." Passing from the Amphibia to the higher forms, RATHKE† believed that this vessel increased in importance, and from supplying the tongue only, as in Amphibia, it became, in Reptiles, Birds, and Mammals, the artery which was distributed to all the external parts of the head, hence its name of "external carotid." But upon close comparison of the arteries in these different groups it becomes evident that this vessel, instead of increasing, diminishes in importance as the higher forms are reached. In Crocodiles it supplies only the trachea and lateral parts of the neck, and is called "arteria collateralis colli." In Chelonian Reptiles its distribution is very similar, and it goes by the name of "common cervical." In Birds it is still smaller, and is recognised simply as a branch of the subclavian or innominate artery distributed to the front of the trachea. In Mammals I am inclined to believe that it is usually absent, but that, when present, it is represented by the artery "thyroidea ima."

The first and second portions of the carotid system, the third arch, and its dorsal continuation forwards, must be considered together, as in most forms it is impossible to draw an exact line of separation between them, owing to the disappearance of the vessel connecting, on the dorsal aspect of the alimentary canal, the third arch with the arch immediately behind it. The names applied to this continuous trunk, formed from the two portions already noticed, are very confusing. RATHKE called it "internal carotid," and believed that it supplied only the brain; but it is obvious, from what has been pointed out with regard to the so-called "external carotid," that this vessel constitutes the whole supply of the head, both internally and externally, and may with propriety be called "common carotid." In the description which follows of the individual vessels in the different groups I have named this vessel "dorsal carotid," pointing out, where it is possible, the line of separation between the portion of it formed from the third arch and that derived from the dorsal prolongation to the head In Amphibia the dorsal carotid supplies the brain and external parts of the head, but is not distributed to the tongue. In all the higher forms it supplies the tongue also, owing to the diminished size of the ventral carotid.

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* RATHKE, "Untersuchungen über die Aortenwurzeln, &c.," p. 80.

† *Loc cit.*, p. 76.

These views as to the supply of the external parts of the head by a dorsal and not, as RATHKE believed, a ventral vessel, may easily be proved by reference to Comparative Anatomy. In some Amphibia the third arches are connected dorsally with the aortæ, and in these forms it is easy to follow the continuous dorsal longitudinal vessels running the whole length of the body. The portions of these in front of the heart form the common carotids, and distribute branches to both internal and external parts of the head. In other Amphibia the dorsal connections between the third and fourth arches are obliterated, but, the other vessels remaining unaltered, it is at once evident by comparison that the common carotid artery represents a dorsal trunk. In some Reptiles the dorsal connections between the third and fourth arches persist either as open vessels or as solid cords, and in others they have completely disappeared; indeed, in different species of the same genera, in which all the other arterial vessels present precisely similar relations, the dorsal connecting cords are present constantly in some and absent constantly in others. In these cases, as in the Amphibia, the continuation of the dorsal longitudinal trunk from the aorta into the common carotid is followed without difficulty. The anatomy of the arteries of Birds is almost an exact counterpart of that of the Crocodile; and, apart altogether from the actual observation of the development, it is evident that the relations of parts are to be explained in a similar manner.

The relations of the subclavian artery are much more simple than those of the carotids. RATHKE* believed that there was but one vessel which in the Vertebrate series gave branches to the limb, but in reality there are two such vessels. One of these arises from the aortic root or dorsal portion of the fourth arch, and stretches outwards in a plane dorsal to the pneumogastric nerve and jugular vein. It is found in Amphibians, Lacertilians, and most Mammals. The other arises from the ventral end of the third arch, and stretches outwards in a plane superficial to or ventral to the nerve and vein. It occurs in Chelonian and Crocodilian Reptiles and Birds. Both are sometimes present in one form, and when found together they anastomose with one another in the lateral body-wall near the base of the limb.

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* RATHKE, *loc. cit.*, pp. 80, 81.

Detailed Description of the Carotid and Subclavian Arteries in different Vertebrata.

AMPHIBIA.—In the Amphibia two vessels pass towards the head, the dorsal and ventral carotids. In some of the forms the third or carotid arch is connected dorsally with the aortic (*Menopoma*), but in others, especially in those where the structure known as the carotid gland is largely developed (*Salamandra*, BOAS),* the dorsal connection between the carotid and aortic arches disappears when the adult stage is reached, but in either case the anatomy of the dorsal and ventral carotid arteries is practically the same. The dorsal carotid, continued forwards from the dorsal end of the arch, distributes branches to the head, which are named by ECKER† in the Frog ascending pharyngeal, ophthalmic palatine, and internal carotid, the last being the portion of the trunk which supplies the brain. The ventral carotid or lingual artery gives branches to the front of the trachea and to the muscles upon the ventral aspect of the neck, and ends in the tongue. Fig. 5, from ECKER, represents the relative positions of these vessels. The lingual, external, or ventral carotid artery is interesting on account of its limited distribution on the under-surface of the neck, extending forwards only to the posterior edge of the oral aperture, in marked contrast to the so-called external carotid of Mammals, which supplies the whole of the outer aspect of the head.

The subclavian artery arises from the aortic root, and in close contact with its base a branch, the occipito-vertebral (*o.v.*), springs, and may be described along with it, as in many of the higher forms they arise by a common stem. The artery is dorsal to the pneumogastric nerve. The occipito-vertebral branch is the most interesting. It divides into two. Its anterior branch, passing forwards, distributes a number of twigs to the back of the head, while the posterior portion, with a direction backwards, gives off several intercostal arteries. The subclavian of the Frog corresponds in origin and position to the artery which in Mammals bears the same name. In Mammals, however, the occipital artery is not commonly found to spring from the subclavian, but in the Porpoise such an arrangement is present. The deep cervical artery of Man, a branch of the subclavian, anastomoses among the muscles of the neck with the occipital artery, and this connection between the two vessels may be looked upon as representing the occipital artery of the Frog. MACALISTER‡ looks upon the occipital

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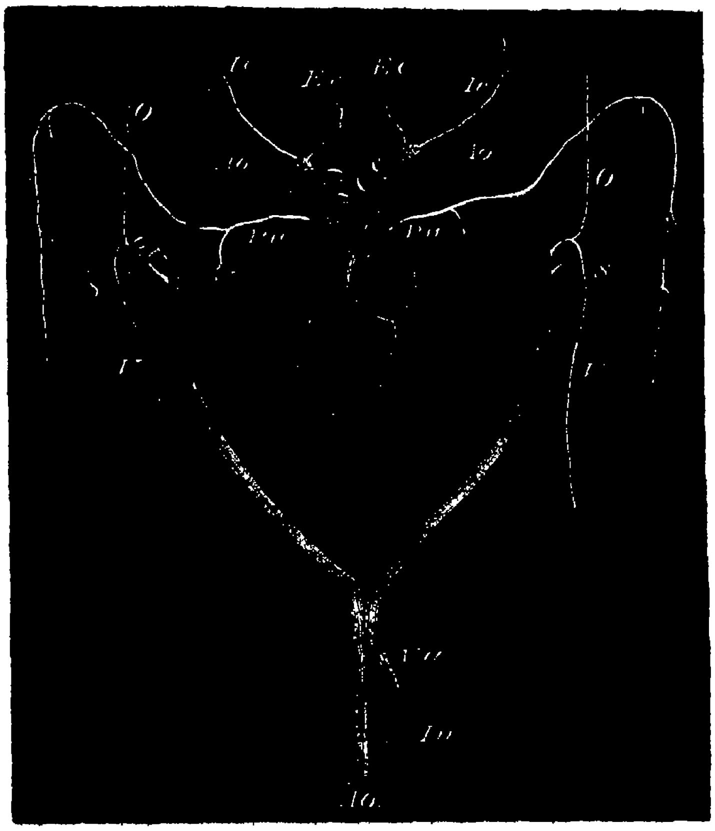
* BOAS, "Beiträge zur Angiologie der Amphibien," 'Morphol. Jahrb.,' vol 8, 1883, pp 169–187

† ECKER, 'Die Anatomie des Frosches,' vol. 2, p. 68, fig. 29. Braunschweig, 1882

‡ MACALISTER, "Morphology of the Arterial System in Man," 'Journal of Anatomy and Physiology,' January, 1886

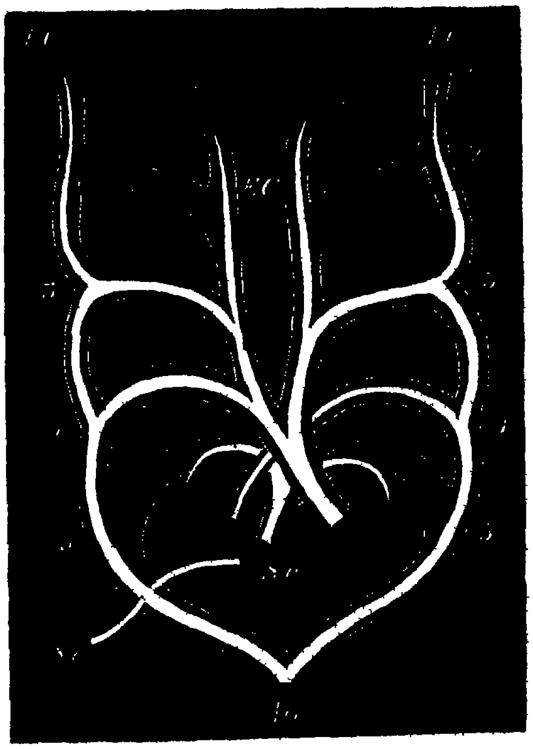
Fig. 5.



Arterial system of Frog (Ecker)

Ao., aorta; *C a.*, carotid arch, *E c.*, external carotid or lingual artery; *I.c.*, branches to internal and external aspects of head; *S*, subclavian; *O*, occipital; *V.*, posterior vertebral or common intercostal; *P.a.*, pulmonary artery with branch to cutaneous surface, *V.a.*, visceral artery, *In.*, intercostal.

Fig 6.



Arches of the Lizard (Rathke).

1, 2, 3, 4, 5, branchial arterial arches; *S.c*, subclavian; *E C*, external carotid; *I C*, internal carotid; *Ao*, aorta.

artery as part of a vascular arch passing from the vessel upon the ventral aspect of the throat towards the dorsal vessel, in the same manner as the carotid, aortic, and pulmonary arches stretch from one to the other. But its connection with the subclavian leads me to believe that it is to be regarded as belonging to the same series as the vessel to the fore-limb in Mammals and some other forms, namely, to that of the vessels running in the somatic wall after the manner of intercostal trunks.

Reptilia. (*a*) *Lacertilia.*—The arterial system of the Lizards resembles in many respects that of the Frog. The aortic and pulmonary arches are present on both sides in all, and in many the carotid arches are connected dorsally with the aortic.

Fig. 6, from Rathke,* represents the scheme of the Lacertilian arrangements. There are many variations in connection with the dorsal communications between the carotid and aortic arches. Plate 25, fig. 34, is a diagrammatic representation of the arches in *Ameiva vulgaris* (Rathke), and shows the dorsal vessel from the carotid arch continued back to the aorta in almost undiminished size. Plate 25, fig. 35,† *Lyriocephalus margaritaceus* (Rathke), presents the connection still patent, but reduced in size very considerably. Fig. 36, *Chamæleo planiceps* (Rathke),‡ represents the connection reduced to a slender cord, and in *Chamæleo vulgaris* (Plate 25, fig. 37), while the arches still retain their relative positions, the connecting link has disappeared altogether In all the varieties, however, the carotid arteries present exactly similar relations. The dorsal carotid artery is continued forwards from the dorsal end of the arch in direct continuity with the connecting cord when that is present, and, even when the connecting cord has disappeared, is still obviously in the same position, and supplies not only the brain, but the whole of the outer aspect of the head. The branches which it divides into may be named "sub-mental," "inferior maxillary," "transverse facial," "occipital," "temporo-facial," and "internal carotid."

A vessel springs from the ventral end of the third arch and extends forwards upon the under-surface of the neck only as far as the posterior margin of the oral aperture, to end in the tongue. On the way it supplies several branches, one of which, marked *s.c.* in Plate 25, fig. 37, is important, as it is that which represents the subclavian in Chelonians, Crocodiles, and Birds. This vessel has been carefully dissected by me in *Chamæleo vulgaris.*§ It passes outwards and backwards to reach the muscles of the shoulder, among which it ramifies, anastomosing there with branches of the subclavian artery. By an enlargement of this anastomotic vessel, if the original root of the subclavian failed, the blood would reach the limb by a vessel ventral to the pneumogastric nerve. This anastomosis probably explains the difference in position of the subclavian in Lizards and Birds. Another vessel, springing from the carotid arch, is worthy of notice. In those forms in which the dorsal connecting trunk between the carotid and aortic arches is still patent there arises from it a small branch which passes into the muscles of the wall of the neck. When the connecting trunk is absent this vessel arises from the base of the dorsal carotid artery In these circumstances it occupies a position similar to that of the supra-scapular artery in Birds, and marks the position of the posterior extremity of the vessel continued forwards from the dorsal end of the carotid arch.

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* Rathke, "Untersuchungen über die Aortenwurzeln, &c.," Taf. vi., fig. 8.

† *Loc. cit.*, Taf. ii., fig 3.

‡ *Loc. cit.*, Taf. ii., fig. 9.

§ "Arterial System of the Chamæleon," 'Glasgow Phil Soc. Proc.,' 1886.

The subclavian arteries in the Lacertilia correspond in origin to intercostal vessels. They spring in close proximity to one another from the right aortic root in a position dorsal to the pneumogastric nerve. The branches given off before entering the arm are "ascending cervical," "internal mammary," and "internal thoracic."

(*b*) *Crocodilia.*—The chief difficulty in comparing the arteries of the Crocodile with those of the Lizard is occasioned by the difference of nomenclature. In all, the aortic and pulmonary arches are present on both sides, and the carotid arches have always been figured as not connected dorsally with the aortic. In a dissection, however, of the vessels of a young Crocodile (*Crocodilus niloticus*), which measured 29 inches, I found the carotid arches completed on both sides by solid cords. The arrangement met with is represented on Plate 25, fig. 33, and presents an exact counterpart of the relations of the arches in *Chamæleo planiceps* (fig. 36). From the carotid arch upon each side two vessels are prolonged forwards; one, passing from the dorsal end of the arch, corresponds with the dorsal carotid of Lacertilia and Amphibia, and is usually called "common carotid" or "carotis subvertebralis"; the other, from the ventral end of the arch, representing the ventral vessel of Lacertilia and Amphibia, is called "arteria collateralis colli," and has associated with it at its base the subclavian artery.

The subvertebral carotid passes dorsalwards round the œsophagus in the same manner as the carotid artery of Birds. The artery of the right side, although present in the embryo, disappears in the adult. In my specimen I found it reduced to a cord arising from the innominate, and passing round the œsophagus to join the vessel of the opposite side in the middle line underneath the vertebral bodies. It was connected dorsally with the aortic arch in the same way as the artery of the left side. The carotis subvertebralis, as it passes forwards underneath the vertebræ of the neck, is thus formed by the junction of the vessels of the right and left sides, which are continued forwards from the dorsal extremities of the carotid arches, and is therefore to be compared to the median aorta, which is similarly formed and passes backwards in a similar position. Near the head the common vessel splits into its two component portions, and these rapidly break up into branches which supply the external and internal parts. RATHKE has named the branches "internal maxillary," "infra-maxillary," "temporal," and "internal carotid" proper supplying the brain.

The arteriæ collaterales colli of RATHKE pass forwards in the ventro-lateral aspects of the neck. They give branches which ramify upon the under-surface of the trachea and in the muscles of the neck, and terminate at the tongue in anastomosis with the infra-maxillary branches of the carotid stems. They correspond accurately with the ventral (external) carotid of Lacertilia (see fig. 37, *Chamæleo vulgaris*), but the branch which in the Chamæleon passed to the muscles of the shoulder has now become subclavian.

The subclavian arteries, arising from the innominate stems, or, in other words, from the ventral ends of the carotid arches, in actual proximity to the bases of the last-described vessels, pass forwards and outwards, crossing on their way, ventral to the carotid arteries, the veins from the neck, and the pneumogastric nerves. Before reaching the arm the internal mammary artery is given off, and also a vessel to join in anastomosis with intercostal arteries. From this anastomosis the vertebral springs. There is thus evidence of the anastomotic connection between the arteries arising on the ventral side of the throat and the intercostal arteries dorsally, which has already been noticed in the Chamæleon.

The arrangement of the large arteries in the Crocodile resembles very closely that found in Birds, the main difference lying in the presence of the fourth or aortic arch upon the left side in the former, while in the latter class it is absent altogether. Plate 22, fig. 3, represents my view of the metamorphosis of the arterial arches in the Crocodile.

(*c*) *Chelonians.*—The anatomy of the great arteries in the Chelonian group is similar in most respects to that of the Crocodile. The aortic and pulmonary arches are present on both sides, but in my dissections in this Order I have never found the carotid arch completed by a dorsal connection with the aortic. The common carotid (dorsal carotid) artery is similar in its origin and distribution to the vessel which bears the same name in Birds and Crocodiles, but differs in its course, inasmuch as it does not pass completely round the œsophagus to reach the middle line, but passes forwards in the dorso-lateral parts of the neck. This is the position which the common carotid occupies in the Mammalian class. The Chelonian group, in the arrangement of the vessels, thus forms an important link between Birds and Crocodiles, upon the one hand, and Mammals upon the other; the distribution corresponding exactly with that of the former classes, the course through the neck with that of the latter. The position which the carotid artery holds in the neck is that which, as has already been shown, it occupies during the earlier stages in the embryo Chick. It is possible that the comparative shortness of the neck may be related to the incomplete development of this trunk in Chelonians and Mammals.

The artery which, running upon the ventral aspect of the throat, corresponds to the ventral carotid of the Frog and Lizard, and to the arteria collateralis colli of the Crocodile, has been named in the Chelonian by RYMER JONES* the "common cervical." This vessel springs from the base of the subclavian trunk, and, coursing forwards underneath the trachea towards the oral aperture, gives many branches to the air-tube and to the ventral aspect of the neck, and ends in anastomosis with branches from the dorsal carotid.

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* RYMER JONES. Article "Reptilia," 'Cyclopædia of Anatomy and Physiology,' by TODD, London, 1852.

The subclavian artery arises on each side by an innominate trunk along with the carotid. It passes forwards and outwards, crossing ventral to the pneumogastric nerve and the jugular vein, as in Birds and Crocodiles. Before it reaches the limb two important branches are given off. The first is the internal mammary. The second is a vessel which supplies some intercostal branches and represents the anastomosis between the dorsal and ventral branches in the somatic wall, already described in the Lizard and Crocodile. From this vessel springs a large dorso-cervical or deep cervical artery, which enters into free communication with the occipital from the dorsal carotid, the anastomotic connection between occipital and intercostal being particularly well marked in this group.

BIRDS.—The arterial system has already been sufficiently described, but a comparison between the individual vessels of this and other groups may be briefly drawn. The pulmonary arches are present on both sides, but the left aortic is absent. The carotid arch is not connected dorsally with the arch behind it, but I have pointed out the occasional presence of a dorsal connection between the two arches (Plate 25, fig. 32). The common carotid (dorsal carotid) is similar in origin, course, and distribution to the subvertebral carotid of the Crocodile. The ventral carotid (arteria collateralis colli of the Crocodile, and common cervical of the Chelonian) is represented by a small vessel springing variably from the innominate, subclavian or base of the carotid stem, ramifying for a short distance upon the ventro-lateral aspects of the neck, and giving branches to the trachea. The subclavian is ventral in position.

MAMMALS.—The anatomy of the carotid system in this class differs in a marked degree from the arrangements found in the classes already described. A common carotid artery, running in the lateral parts of the neck, divides into two stems—an internal and an external carotid, the former being in many cases entirely devoted to the supply of the brain, the latter to the whole of the external aspect of the head. RATHKE* has described the development of these vessels, and holds the common carotid artery to represent the ventral trunk between the carotid and aortic arches, the external carotid being the continuation of this ventral trunk still further forwards, and the internal carotid the third arch and the dorsal continuation towards the head, fig. 7.†

In addition to the embryological evidence with which RATHKE supports his scheme, it seems probable that the special development of the brain for which this class is peculiar may have determined the whole of the blood-supply of the dorsal carotid to that organ. The ventral carotid, which in all the other groups examined was represented by a vessel of small size running forwards, never beyond the oral aperture, has been shown in the previous descriptions to maintain an anastomosis with branches of the dorsal carotid, and it is possible that, by virtue of this connection, the whole of the external branches of the dorsal vessel may have been transferred to the ventral. In the Ground Hornbill (*Bucorvus abyssinicus*), where the dorsal carotids are represented in the whole of their subvertebral course by solid cords, the passage of blood to the head is maintained by an anastomotic vessel occupying the position of the arteria collateralis colli of the Crocodile, which joins in front one of the maxillary branches of the dorsal artery. In this case, therefore, by a secondary change, shown to be so by the fact that the dorsal carotids are still present as solid cords, the whole of the blood-supply of the head passes through the neck by way of the ventral vessels—an arrangement similar to that which is expressed in the explanation which RATHKE has put forward of the Mammalian development.

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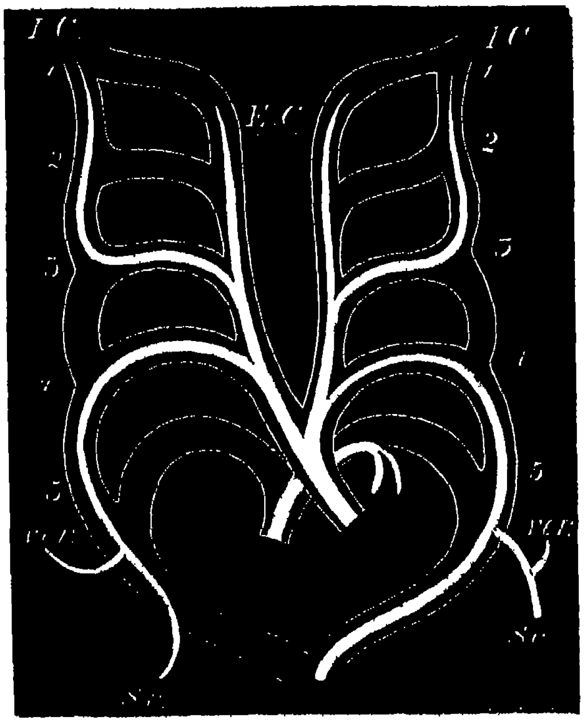
* "Ueber die Entwickelung der Arterien, welche bei den Säugethieren von dem Bogen der Aorta ausgehen." 'MÜLLER, Archiv Anat. Physiol.,' 1843, pp. 276–302.

† RATHKE, "Untersuchungen über die Aortenwurzeln, &c.," Taf. vi., fig. 10.

Fig. 7



Arches of the Mammal (RATHKE)

1, 2, 3, 4, 5, branchial arterial arches; *S.c.*, subclavian; *ver.*, vertebral; *E C.*, external carotid; *I.C.*, internal carotid.

On the other hand, it seems more probable, judging from Comparative Anatomy, that the common carotids of Mammals represent the dorsal carotids of other forms, the branch which supplies the brain being specially enlarged so as to seem the continuation of the parent trunk. The ventral carotid artery, which in the passage from Amphibians to Reptiles and Birds has been shown to diminish in size and importance, would be in this scheme absent altogether in most forms, but constant in some (Porpoise, fig. 38) and occasional in others as the thyroidea ima artery. It is also interesting to note that when, as sometimes happens, the common carotid artery in Man is absent, and the external and internal carotids arise separately from the arch of the aorta, it is the internal carotid which occupies at its origin the more anterior or ventral position. I have not had an opportunity of examining the development of the carotid arteries in Mammals, but I believe that a further investigation is necessary.*

The Mammalian subclavian artery usually springs from the aortic arch, as in the Lacertilian, and its further development has been described by RATHKE. This is not always the case, however. In a paper upon the arterial system of the Porpoise † I have pointed out that the artery which in that animal represents the subclavian of other Mammals does not supply branches to the fore-limb, but is distributed entirely as an intercostal vessel (Plate 25, fig. 38). The artery which supplies the limb occupies a position ventral to the pneumogastric nerve, and expresses the subclavian artery of Birds, so that in this form the two representatives of the subclavian artery found in the Vertebrate series are present. From a description of the arteries of the Narwhal by SEASON WILSON‡ it is evident that the arrangements in that form are similar to those in the Porpoise, so that it is probably true of the Cetacean division generally.

Summary of Comparative Anatomy.

In all forms lower than Mammals and above Fishes a dorsal and a ventral carotid artery are recognisable. The former represents the third arch and its dorsal continuation forwards; it supplies branches to the brain and to the whole of the external parts of the head, except, in the lower forms, the tongue. In certain instances (Birds and Crocodiles) it passes forwards in the middle line immediately underneath the bodies of the cervical vertebræ, the vessels of opposite sides being either in contact with one another (Birds) or fused into a median trunk (Crocodiles). In other cases (Amphibia, Lacertilia, Chelonia) the dorsal carotids are separated from one another, and lie underneath the transverse processes of the vertebræ. In spite of the difference, of course, in the cases above mentioned, the arteries are identical in origin and distribution.

The ventral carotid supplies the tongue in Amphibian and Lacertilian forms, but is reduced in Chelonia and Crocodilia, and does not extend so far forwards as the oral aperture. In Birds it is a slender vessel supplied to the ventral surface of the trachea.

There are two vessels which in different cases may give origin to the subclavian artery. One of these is ventral in origin, and passes out in front of the pneumogastric nerve; the other is dorsal, and crosses behind the nerve. They anastomose with one another in the body-wall. The ventral artery is found in Chelonian and Crocodilian Reptiles, in Birds, and among Mammals in the Cetacean group. The dorsal vessel is enlarged and prolonged into the limb in Amphibians, Lacertilian Reptiles, and in all Mammals, with the exceptions already noted.

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* From the researches of HIS ('Anatomie menschlicher Embryonen,' Leipzig, 1880) it is evident that in early human embryos the ventral carotid reaches as far forwards as the tongue and lower jaw, but it is possible that in subsequent development the origin of the vessels for these parts may be transferred, as in Birds, to the dorsal root.—[September 21, 1887.]

† "Arteries of the Head and Neck of the Porpoise, &c.," 'Glasgow, Phil. Soc. Proc.,' 1886.

‡ WILSON, 'Journal of Anatomy and Physiology,' 1880.

In concluding, I have to offer my thanks to Professor CLELAND for much valuable assistance, and for placing a large number of specimens at my disposal for examination or dissection, to Dr. BRUCE YOUNG for help in the preparation of the plates; and to Mr. CAMPBELL, of the Glasgow Museum, for a large number of Birds for dissection.

DESCRIPTION OF PLATES 22–25.

Fig. 1 (Plate 22) View from behind of Heart and Vessels of Nandu (*Rhea americana*).

Ht.	Heart.
Ao.	Aorta.
pa.	Pulmonary artery.
l.d.a.	Left ductus arteriosus.
r.d.a.	Right ductus arteriosus.
l.c.	Left carotid.
l s.	Left subclavian.
r.c	Right carotid.
r.s.	Right subclavian.
p.v.	Pulmonary vein.

Figs. 2 and 3 (Plate 22). Scheme of the metamorphosis of the Arches in Birds (2) and Crocodiles (3).

I., II., III., IV., V.	The arches.
C.C.	Common carotid.
S.	Subclavian.
Ao.	Aorta.
P	Pulmonary artery.
A.c.c.	Arteria collateralis colli.

Fig. 4 (Plate 22). Arches of Embryo at close of fourth day.

Ht.	Heart.
Ao.	Aorta.
C.	Carotid.
S.	Subclavian.
V.C.	Cardinal vein.
m.	Mandibular bar.
h.	Hyoidean bar.

Figs. 5–30 (Plates 22–25). Sections of Chick embryos.

Figs. 5–10. Transverse sections through anterior portion of body, at the close of the third day (the sections are slightly oblique). They succeed one another in order, and are taken from a series, of which No. 5 is the

7th, 6 the 10th, 7 the 14th, 8 the 17th, 9 the 18th, and 10 the 19th.

br.	Brain.
n.	Nerve.
v.	Vein.
d a.	Dorsal artery.
ret.	Retina.
n.c.	Notochord.
v.a.	Ventral artery
ph.	Pharynx.
per.	Pericardium.
tr.a.	Truncus arteriosus.
ht.	Heart.
s.	Subclavian artery.
a.	Arch.
au.	Ear.

Figs. 11–14. Longitudinal antero-posterior (sagittal) sections, at the close of the fourth day.

Figs. 11 and 12 are carried through the right side, fig. 11 being the more superficial.

Figs. 13 and 14 are carried through the left side, fig. 13 being the more superficial

a. 3.	Third arterial (carotid) arch	right side.
a. 4.	Fourth arterial (aortic) arch	
a. 5.	Fifth arterial (pulmonary) arch	
a'. 3.	Third arterial arch	left side.
a'. 4.	Fourth arterial arch	
a'. 5.	Fifth arterial arch	
au.	Ear.	
v.	Vein.	
al.	Alimentary canal.	
ht.	Heart.	
s.	Subclavian.	
d.c.	Dorsal carotid.	

Figs. 15–16. Vertical transverse (frontal) sections, at the close of the fourth day; fig. 15 is the anterior.

a. 3.	Third arch.
a. 4.	Fourth arch.
a. 5.	Fifth arch.
ao.	Aorta.
d.c.	Dorsal carotid.

Figs. 17–26. Vertical transverse (frontal) sections, at the close of the fifth day; fig. 17 is the 2nd of the series, 18 the 3rd, 19 the 4th, 20 the 7th, 21 the 8th, 22 the 10th, 23 the 14th, 24 the 15th, 25 the 16th, and 26 the 17th.

Figs. 17–19. Sections across the truncus arteriosus, which, while undivided on the surface, shows on section at this stage a set of canals continuous with the arches

$$\left.\begin{array}{l} a\ 3. \\ a.\ 4. \\ a.\ 5 \end{array}\right\}\text{Arches of the right side.}$$

$$\left.\begin{array}{l} a'.\ 3. \\ a'.\ 4. \\ a'.\ 5. \end{array}\right\}\text{Arches of the left side.}$$

In figs. 17 and 18 a'. 3 and a'. 4 are fused into one canal.

Figs. 20–26. Arches as in figs. 17–19.

br. Branch from the third arch
v. Vein.
al. Alimentary canal.
d.c. Dorsal carotid.
ver. Vertebra.
ao. Aorta.

Figs. 27–30. Vertical transverse sections in the earlier stages of the sixth day.

Fig. 27 is carried through the truncus arteriosus, which is still undivided externally.

Figs. 28–30 show the arches as they pass in a dorsal direction.

The references are the same as in the series 17–26.

Fig. 31 (Plate 25). Arches on left side of Chick, at the close of the sixth day.

III., V. Third and fifth arches; the fourth has disappeared.
T.A. Truncus arteriosus.
P. Pulmonary artery.
S. Subclavian.
C.c. Common carotid.
D.B. Ductus Botalli.

Fig. 32 (Plate 25). Adult Guillemot (*Uria troile*); persistence of ductus Botalli between common carotid and aorta, upon the right side.

l.d.a. Left ductus arteriosus.
Ao. Aorta.
D.B. Ductus Botalli between right carotid and aortic arches.
c.a. Common carotid artery.
al. Alimentary canal; *r.l.* Right lung; *l.l.* Left lung.

Fig. 33 (Plate 25). Heart and arches of *Crocodilus niloticus*
S. Subclavian arteries.
C Carotid arch.
A. Aortic arch.
P. Pulmonary arch.
Ductus Botalli connect *C.* and *A* , and *A* and *P.*

Fig. 34 (Plate 25). Carotid and aortic arches of left side of *Ameiva vulgaris* (Rathke)
Ao.A. Aortic arch.
C.A. Carotid arch.
c l. Cervico-lingual artery.
C. Branches to internal and external aspects of Head.

Fig. 35 (Plate 25). Carotid and aortic arches of *Lyriocephalus margaritaceus* (Rathke), right side. Lettering as in fig 34.

Fig. 36 (Plate 25). Carotid and aortic arches of *Chamæleo planiceps*, right side (Rathke). Lettering as in fig 34.

Fig. 37 (Plate 25). Carotid and aortic arches of *Chamæleo vulgaris*, right side
T.a. Truncus arteriosus.
R.a.r. Right aortic root.
L.a.r. Left aortic root.
C.a. Carotid arch.
L c.a. Left carotid arch.
C. Carotid artery; *C.e.* External carotid; *C i.* Internal carotid.
C.l. Cervico-lingual artery; *Sc.* Scapular branch; *l.* lingual; *h.* hyoid.
S.r. Right subclavian artery , *S.l.* Left subclavian.
In. Intercostal arteries.
Ao. Aorta.

Fig. 38 (Plate 25). Arteries of the Neck and Thorax of the Porpoise.
In. Innominate artery.
B.c. Brachio-carotid.
C. Carotid; *C.e.* External carotid; *C.i.* Internal carotid.
h. Hyoid; *l.* Lingual; *oc.* Occipital.
S. Subclavian artery; *th.* Superficial thyroid branch; *as c* Ascending cervical; *sc.* Scapular; *oc.* Occipital; *e.t.* External thoracic; *i.m.* Phrenic and internal mammary.
Br. Brachial.
d.th. Deep thyroid artery.
P.t. Posterior thoracic; *d.* Its dorsal branch.
i.i Intercostal arteries.
On the right side a portion of the thoracic rete is shown.
pn. Pneumogastric nerve.

V. *Researches on the Structure, Organization, and Classification of the Fossil Reptilia.—III. On Parts of the Skeleton of a Mammal from Triassic Rocks of Klipfontein, Fraserberg, South Africa* (Theriodesmus phylarchus, SEELEY), *illustrating the Reptilian Inheritance in the Mammalian Hand.*

By H. G. SEELEY, *F.R.S., Professor of Geography in King's College, London.*

Received October 24,—Read November 24, 1887

[PLATE 26]

AMONG specimens collected from various localities in Cape Colony by Mr. THOMAS BAIN, and deposited in 1878 in the British Museum of Natural History, is a small counterpart slab, 8 inches long by 5½ inches wide, now registered under the number 49,392. It was labelled by its discoverer "The hand of a Saurian, from Klipfontein, Fraserberg, South Africa"; and this determination escaped question. Its exact geological horizon is unfortunately unknown, but is probably the same as that of the Dicynodont Reptiles collected with it, which are on many grounds regarded as Triassic. This slab is a natural mould of the bones of the fore-limb of one of the smaller Mammalia characterised by five digits. It also shows, in less satisfactory preservation, remains of the tibia and fibula, which are relatively longer than the corresponding bones of the fore-limb. The animal thus indicated was considerably larger than the Otter, and approximated to the dimensions of the Wolverine. In their general shape and elongation, the limb bones, as a whole, approximate to the smaller Carnivora, but are distinguished by many differences of detail. Thus, the bones of the fore-arm are more nearly equal in size, though the difference is one of degree rather than type; and the same is true of the bones of the fore-leg. But, except the tibia, and possibly the humerus, none of the bones give evidence of having terminated in epiphyses, and the forms of the distal ends of the ulna and radius are unlike those found in Carnivora. The carpus also shows some new points, though the bones are displaced, in giving evidence of a third row of carpal bones. The phalangeal bones of the digits, also, vary from the usual Mammalian type, and possibly, in one digit, give evidence of renewal after the digit had been lost, as among Amphibians. The vertebral column is only indicated by a portion of a single caudal vertebra. None of the differences, however, which the specimen shows from the skeletons of existing

23.7.88

Mammals can be regarded as making an approximation towards lower Vertebrates in the plan of the skeleton, or as throwing a doubt on the interpretation of the animal as a typical Mammal; but as evidences of inheritance, the carpus, metacarpus, and digits are singularly suggestive. I would express my thanks to Dr. HENRY WOODWARD for permission to study and describe this remarkable fossil, and for his assistance in preparing the beautiful cast from the slab which was made by Mr. HALL, the mason, after the specimen had been cleared from some fragments of the original bone which adhered to the natural mould.

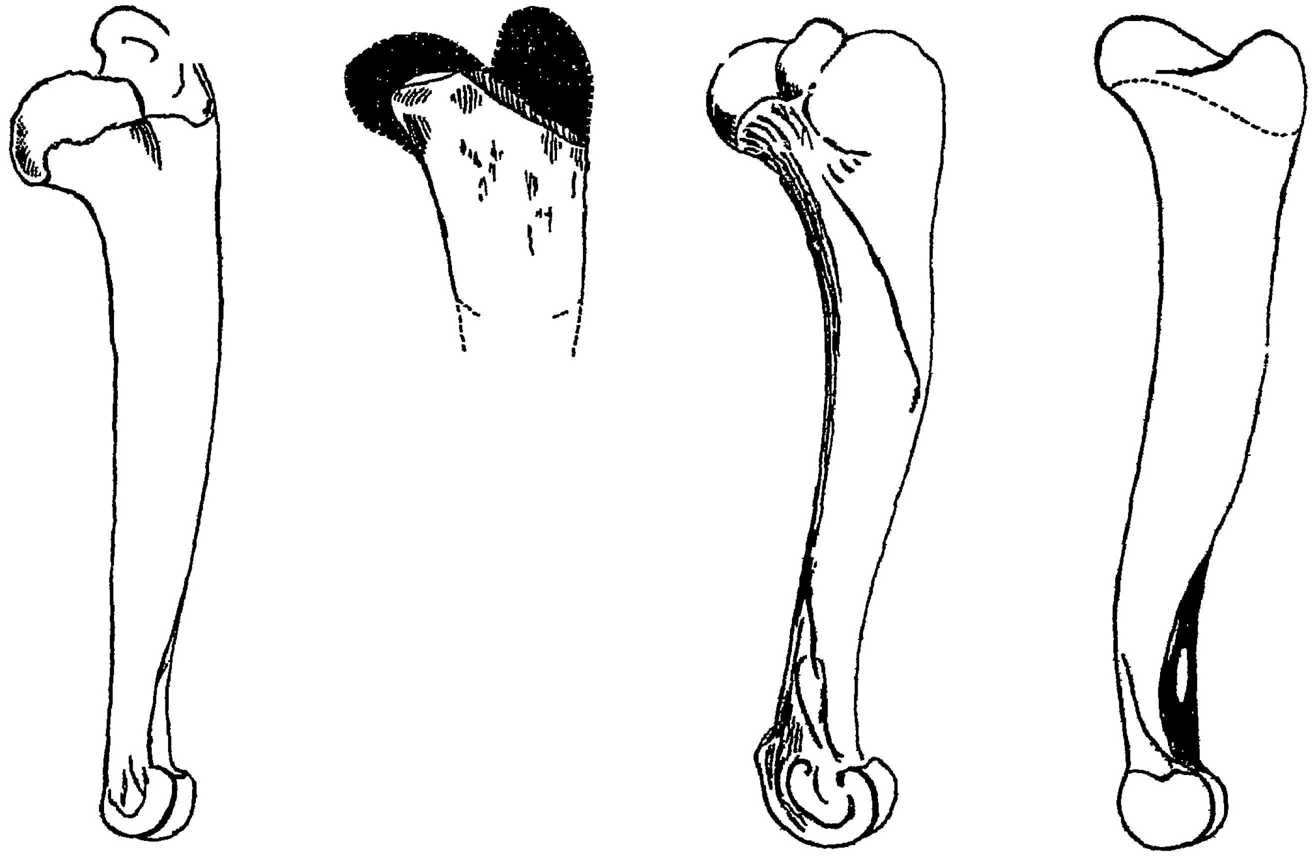
The Humerus

In the impression from the slab the humerus is crossed by the tibia and fibula, so that only its proximal and distal parts are shown: the middle parts of the shaft have been contained in the corresponding slab. The bone is 11·5 centims. long. It is twisted, so that the proximal end is turned inward at an angle of about 45°. Hence the distal end is shown in profile from the outer side, while the proximal end shows the expanded width of the bone, which is comparatively flattened, with a moderate side-to-side convexity. The part of the proximal end which is exposed has an antero-posterior extent of 4·1 centims. It is nearly straight on the anterior border, slightly concave on the posterior border, 3·2 centims. wide at the proximal end as preserved, and 1·7 centim. wide at the distal limit of the exposure. The proximal contour, owing to the shallowness of the impression probably, gives but an imperfect conception of the form of the proximal end of the bone. The proximal articular surface is very imperfectly preserved. What remains of it is convex from front to back, and 2 centims. wide. Its anterior extension is apparently compressed on the ulnar side, with the small hemispherical convexity of the articular head in the middle, somewhat thickened and extended inward, so as to rise convexly above the surface of the impression. Anterior to this boss is a saddle-shaped depression, concave in length and concave transversely, and then a small trochanteroid process rises, which extended to the border of the bone.

The distal exposure of the humerus shows its thickness to have exceeded 7 millims. The fragment seen is 3·1 centims. long. The anterior and posterior sides are subparallel till the distal extremity is reflected forward in the trochlear condylar articulation. The inner surface of the bone is somewhat flattened, and marked by a groove which ascends from the median lateral extremity of the distal condyle, and, extending upward and backward with a slightly concave curve for 2 centims., obliquely crosses the shaft. The slight elevation of this ridge causes all the distal part of the bone posterior to it, which forms the convex posterior part, to be wider transversely than the part of the shaft in front of it. This ridge is not closely paralleled by any structure known to me in the distal end of any humerus. Its direction is the reverse of the band which extends over the epicondylar humeral foramen in many Mammals, though it coincides with the direction of the vessel which such bars cover in

Marsupials and other Mammalia. Because it occurs on the outer side of the bone, I am led to interpret it as comparable to ridges similarly placed in Carnivora. The antero-posterior thickness of the distal end through the condyle is 1·3 centim.; and the vertical extent of the condyle on the anterior side of the bone is 1 centim. The condylar surface is well rounded from above downward and backward.

Diagram showing the right humerus in Mammals which resemble *Theriodesmus.*



Hyrax capensis. *Theriodesmus.* *Felis leo.* *Thylacinus.*

I cannot but suspect the possibility of this humerus having lost its proximal epiphyses; and, if so, the restoration of the missing portions might bring the bone into close correspondence with the Mammals, which it resembles in its distal end. In the outline here given a sufficiently close approximation may be seen to three Mammalian types to be suggestive of affinities. In form the bone is very like the humerus of a Leopard, in which there is a not dissimilar attenuation of the shaft distally; but this character is probably of small importance, since other Felidæ do not show quite the same proportions. And, while some of the Felidæ show a not dissimilar ridge on the outer side of the bone at the distal end, there is also a strong anterior tricipital ridge at the proximal end, to which the fossil offers no approximation. This ridge, however, assumes a more anterior marginal position in some Carnivora, and in others is less conspicuous; still its absence appears to show that the muscular relations of the humerus to the body were not identical with those of existing Carnivora. The resemblance to *Hyrax* is not less remarkable, though now it is the distal ridge that is wanting. A third resemblance is found in *Thylacinus*, which in general form and character of the bone, and especially in the antero-posterior distal compression of the shaft, approximates to the fossil closely.

Ulna and Radius.

The ulna and radius are moderately elongated, but are somewhat shorter than the humerus. The two bones combine proximately to form a semicircular cavity for the distal end of the humerus to work in. This condition is characteristic of Mammals, since the humeral articulation is chiefly due to the prolongation of the ulna proximally into an olecranon process, which extends beyond the articulation in a way which is not found in other Vertebrates. The radius is rather the stouter bone at the proximal end, where it is placed in front of the ulna.

The length of the radius is 8·5 centims. The shaft is straight, moderately constricted in the middle, and somewhat expanded towards the proximal and distal ends. The internal side of the bone is well rounded, and, owing to the constriction of the shaft, its convexity is necessarily greatest in the middle. The posterior side of the bone is rather less concave in length than the anterior border, for the posterior side of the bone appears to be flattened, while the anterior border at the distal end, though convex, is rather compressed. At a distance of 2·6 centims. above the distal end there appears to be a long vascular foramen in the bone near the inner anterior border, but in this region the bone is a little crushed. The articulations of the bone are necessarily only seen in side view, and both proximally and distally are rather less wide than the adjacent part of the shaft. The width of the proximal end of the bone is 14 millims., but external to the articulation the bone expands in a convexity which is almost a process, which overlaps the ulna. The superior extremity of this convexity extends for 4 or 5 millims. further proximally than the anterior border, so that, while the anterior and lateral borders are sharp and well-defined, the articular surface is concave and inclined obliquely forward. This concavity, like that of the adjacent ulna, is parallel to the convexity of the distal articular end of the humerus, from which it is separated by an interspace as if for cartilage about 2 millims. wide.

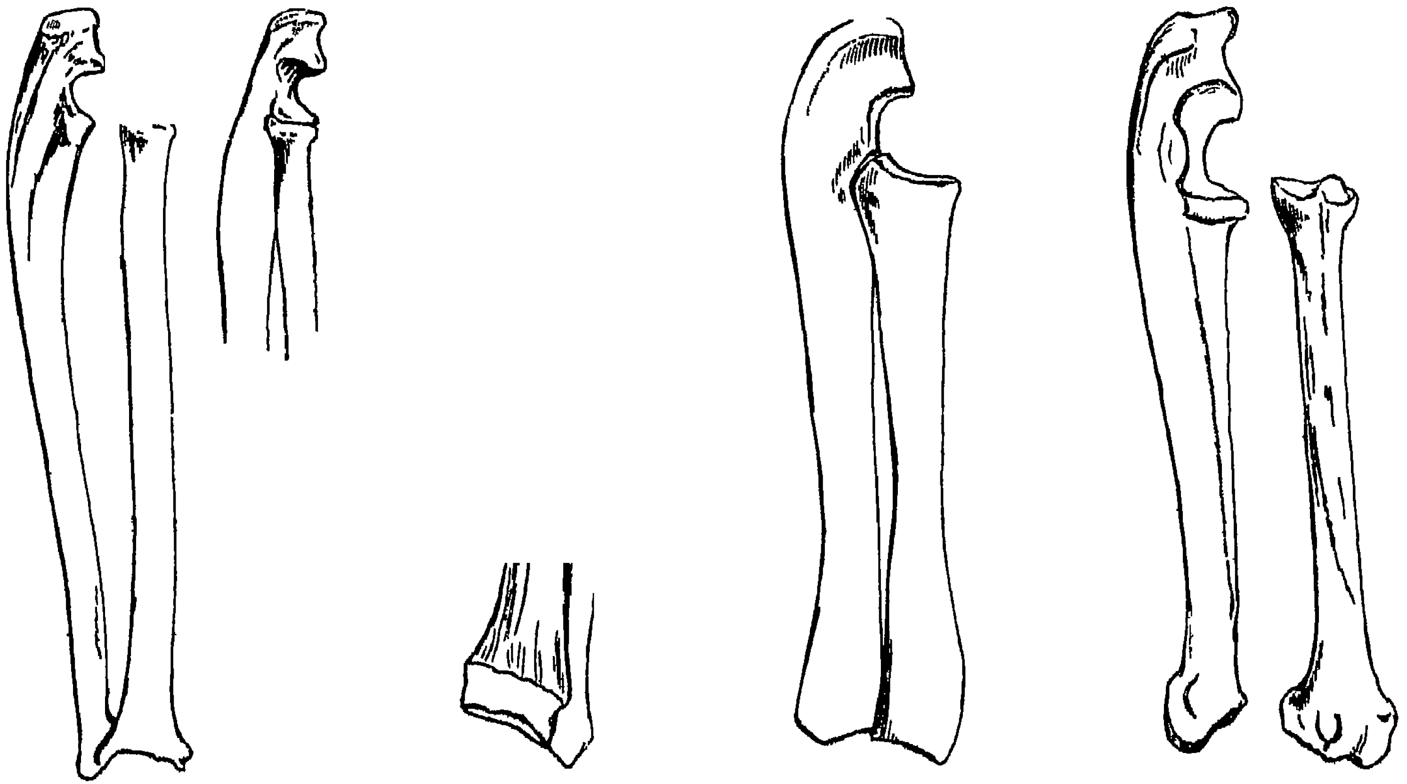
The distal articulation is somewhat similar in character, except that the less prominent distal convexity and downward prolongation of the bone is on the inner border, while the shaft is concave on the ulnar side. The side to side width of the articulation is only 12 millims. In this direction the articular surface is concave and oblique, looking downward aud outward, because the inner border has a greater extension distally than the ulnar border. The margin of the articulation is sharp, and the surface is transverse to the shaft.

The ulna is a straight bone, somewhat compressed from side to side. It is 10 centims. long, and in form and extent of the olecranon process approximates to the ulna of the Wolverine and some of the smaller Carnivora. Its shaft has a slight curve by which the middle part bends inward towards the radius, while the greater part of the proximal end of the bone is behind the radius. Distally the ulna is displaced so as to lie away from the radius and most of the carpal bones. The impression of the ulna in the stone is less deep than that of the radius, so that it is impossible to be sure that the entire width of the bone is exposed, and no estimate can be formed of its thickness. The anterior border of the shaft, below the olecranon articulation, is very slightly convex in length, and the corresponding posterior and external border is rather more markedly concave, for the middle part of the shaft contracts in diameter, though not so conspicuously as the radius. The width of the distal end of the bone is about 11 millims., that of the middle of the shaft is 7 millims., and below the proximal articulation, where the bone is overlapped by the radius, the transverse measurement is fully 11 millims. Its surface is slightly crushed, flattened, and gently convex from side to side. Proximally towards the olecranon, the posterior contour is convex for nearly half the length of the bone, and the convexity augments proximally till it curves round towards the humerus, above the articulation. This part of the ulna extends proximally for 2·4 centims. beyond the middle of the articular surface of the radius. This posterior margin is rounded from side to side, and has every appearance of being compressed as in ferine Mammals. The articular margin is transversely thickened, so as to slightly channel the side of the olecranon process, and distally this thickening abuts against the radius, and so contributes to form the continuous curve of the humeral articulation. The transverse width of the bone at the articulation is fully 11 millims. There is some slight indication that a median ridge ran up the articular concavity which extends upward and forward. Above the articulation the olecranon is truncated in a straight line with a slight obliquity; here it is 1 centim. deep. It extends some distance over the distal end of the humerus, in which there must have been a considerable olecranon pit. Thus the ulna and radius combine to make a perfect hemispherical cup for the humerus, which is nearly 16 millims. wide and inclined obliquely backward.

The distal end of the bone is truncated, and the oblique surface in which it terminates gave attachment to two carpal bones, which are smaller than the single carpal which was attached to the radius.

When these bones are compared with those of other Mammalia, no one genus combines all their characters. In general aspect they are like the same bones in the Wolverine, except for the simpler forms of their distal extremities. The proximal end of the radius perhaps finds its nearest parallel in the Aye-aye and other Lemurs, in which there is a similar concave oblique surface. The ulna is perhaps more like that of *Meles* or *Gulo*. But the distal ends are unlike the corresponding surfaces of Lemurs or Carnivora, and the simplicity of the surfaces is almost Reptilian. Still Mammals like the *Hyrax* make an approximation in the form of the distal ends, which is the more interesting from the somewhat *Hyrax*-like form of the humerus, though there is no close resemblance in form or proportion between the bones of the fore-arm in the two types, and both Sirenians and Seals approximate to the fossil in the form of the distal ends of the ulna and radius. But, whatever may be the taxonomic value of these resemblances in the distal ends of the bones, their predominant characters otherwise suggest Civets, Weasels, and Badgers, with frequent reminders of the bones in Lemurs and Monkeys.

Diagram of ulna and radius.

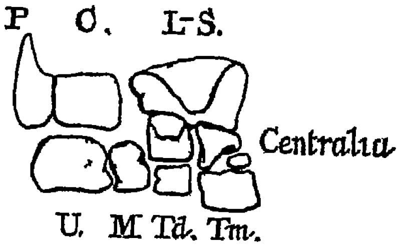


Cheiromys. *Hyrax capensis.* *Theriodesmus.* *Meles.*

The Carpus.

Although the carpal bones are not in compact articulation, they are so displaced as better to show the forms of the bones without disordering their relations The distal row of four carpal bones remains in contact with the metacarpus. Two carpals are in contact with the ulna, and one with the radius, and these form the proximal row. But between these two rows is a portion of the third row, consisting of three bones which are towards the radial side. The largest, and most centrally placed, may be identified with the centrale of Monkeys, Lemurs, and some other Mammalia; but the other bones external to it, on the radial side, rather suggest the condition in the carpus of some Chelonians and Amphibians, and appear to throw some light on the relation of the carpus to the tarsus in Mammals.

The large bone, which is equal in size to the distal end of the radius, and is in contact with it, I regard as the scapho-lunar; and two bones, which are faintly outlined in contact with the ulna, would then be the cuneiform and pisiform bones. The four bones of the distal row of the carpus, being *in situ*, are easily identified as the trapezium, trapezoid, magnum, and unciform bones. There is no possibility of the row having included more bones, since the unciform bone supports two metacarpals. The intermediate row may be distinguished as centrale 1, 2, and 3. This interpretation may be better understood from the following diagram, in which I have made a restoration of the scheme of the carpus.



Scheme of the carpus of *Theriodesmus* restored

The scapho-lunar bone is so far displaced by being twisted forward on the ulnar side that much of its proximal surface is exposed. It is a sub-quadrate bone, and, like all the other carpal elements, has its articular margins sharp and well defined. The proximal surface is 12 millims. wide, smooth, with a cartilaginous articulation which is defined by a linear margin. It is convex from back to front, in harmony with the concavity at the distal end of the radius. The distal surface is somewhat smaller, and develops a prominent mammilate convexity in the middle. The external surface, which was towards the ulnar side, is only 3 millims. deep, concave vertically, convex transversely, with prominent superior and inferior margins, and it shows a few vascular foramina in the middle. The other external surface has a vertical depth of about 9 millims., but diminishes in depth as it extends forward. It is flattened, but is slightly concave both from above downward and behind forward; the measurement in the latter direction is 7 millims., and is limited laterally by a vertical ridge.

The bones which articulate with the distal end of the ulna are much less perfectly indicated, showing only ill-defined impressions of their lateral contours. First, there is a transversely oblong bone on the side towards the radius, which is the cuneiform. It measures a centimetre from back to front, and is 7 millims. deep, and articulates with the principal distal facet of the ulna. The other carpal, adjacent to it, I regard as the pisiform bone. It is a sub-triangular or pear-shaped bone, which has its chief extension behind the ulna. Its transverse measurement is about 6 millims., and its vertical measurement about 1 centim., terminating proximally in a point. These three bones now described I regard as forming the proximal row of the carpus, because, if the distal end of the ulna were brought into contact with the radius, the cuneiform bone would be in contact with the lunar side of the scapho-lunar.

In the distal row, beginning on the inner side, the bones Tm, Td, M, U, present a type common among pentadactylate Mammals, in which the first three bones each support one metacarpal, while the last two are supported by the unciform bone. The trapezium is sub-quadrate or somewhat lozenge-shaped, flat, inclined inward, and measures 5½ millims. in height and breadth.

The external surface of the trapezoid is much smaller, being only about half the width of the proximal end of the second metacarpal on which it rests. Its proximal and distal surfaces are convex, its sides are flattened; it is about 4 millims. high and 3 millims. wide.

The magnum is a larger bone, being 5 millims. wide and 7 millims. high, with the proximal surface prominently convex, and the upper half of its quadrate anterior aspect triangularly excavated, a condition which is paralleled in the magnum of many Carnivora.

The unciform bone is the largest in the distal row Its lateral aspect is sub-quadrate, being about 8 millims. deep and 7 millims. wide with the inner distal angle prolonged as a slight talon, and the outer proximal angle is rounded. The superior and external borders are convex in length, and the external surface is concave.

Between these bones, forming the distal row and the proximal row, is the intermediate row of three bones which was placed on the radial side. There are one or sometimes two bones in this position in the carpus of Chelonians, and at least one in the carpus of Lemurs, of certain Quadrumana, and of some Rodents like the Beavers, while the centrale is a well-known element in the carpus of Salamanders. But in no Vertebrate have three bones been found in the position described.

The first bone (*g*) of this series, counting from the radial side, is situate at the upper inner angle of the trapezium. It is a small ossification, 2 millims. in diameter, and sub-quadrate in form. It may be connected distally with a minute ossification external to the trapezium

The second bone (*h*) is triangular. As preserved, it rests by its flat distal surface upon the trapezium and trapezoid, while the two inclined proximal faces, which are about equal in size, meet to form a sharp pent-house ridge. It is 8 millims. long, and half as high. It is obviously displaced, and one of its superior surfaces was received under the internal half of the scapho-lunar bone.

The third bone (*i*) is much larger than the others, and of sub-quadrate form. It is 8 millims. high, about 7 millims. wide distally, and 4 millims, wide proximally. The proximal surface is flattened to articulate with the lunar portion of the scapho-lunar bone. The distal surface may have fitted upon the trapezoid or the magnum. Laterally the bone has two surfaces, separated by a sharp vertical oblique ridge. The surface on the ulnar side is concave in the vertical antero-posterior direction, and convex from front to back. The other lateral surface faced towards the second centrale already described.

I regard these three bones collectively as homologous with the naviculare in the tarsus. That bone is situate between the astragalus and the three cuneiform bones which carry the first three metatarsal bones, so that the naviculare, originally, may also have included three ossifications. Since the third central bone in this fossil is the largest, that fact may help to account for the internal position taken by the representative ossification in Mammals in which it is still found. This carpus is more primitive than any Mammalian carpus hitherto known, and, on the whole, better compared with that of Amphibians and Reptiles. Dr. R. WIEDERSHEIM, in a paper * on the central bones in the carpus and tarsus in the Axolotl, shows some remarkable conditions of the carpus to be developed with age There are at first three bones in the proximal row, and four bones in the distal row, though ultimately the latter series numbers five † on the left side of the body. Between these rows is the centrale, at first single, and ultimately represented by two cartilages on one side and three on the other I should desire to see preparations before affirming that a linear series of three central elements is a normal characteristic of the Axolotl, but this number appears probably to be present. The presence of two central bones in certain Reptilia is much better established. Dr. FRANZ BAYER has figured and described ‡ two central elements in the young *Hatteria* which have a linear arrangement, and are placed above the second and third tarsals of the distal row. And this condition appears to have been observed independently by Dr. G. BAUR and by M L. DOLLO. It is among Chelonians, however, that the two centralia are most strikingly developed in linear arrangement towards the radial side. But, though the condition of the carpus in this fossil is thus shown to be Amphibian and Reptilian, it is typically Mammalian in all points except that of the central bones. But no Mammal shows more than one central bone, and the number of types in which that one is persistent throughout life is not large. Dr. G. BAUR, indeed, affirms § that a centrale has been shown to occur at some period of life in all orders of Mammals except Ungulata and Cetacea, but figures and detailed descriptions have yet to be given to demonstrate the proposition for some orders. Perhaps the carpus of *Cheiromys* nearly parallels *Theriodesmus*, except that in the Lemur the scaphoid and lunar bones are not united. The one large centrale is in contact proximally with the scaphoid and lunar, and it meets all the bones of the distal row. The bone is relatively smaller in the Orang-utang, but the structure is the same. VROLIK remarks ‖ that this bone is found in the Gibbons, and appears to exist in all the lower Monkeys. VROLIK also figures (*loc cit.*, p. 204) a second ossification between the trapezium and scaphoid, regarded by him as a sesamoid bone for the tendon of the adductor longus pollicis. BAUR (*loc. cit.*) states that he has evidence of the centrale in Man, the Cat, and Dog. In the embryo of *Lutra* the central bone was quite free and very fully developed, while the radiale and intermedium [= scapho-lunar] were coalesced. *Hyrax capensis* has a free centrale, though it is only free in this species of the genus. The presence of this bone cannot but mark an ancient connection between the orders in which it is found; just as the two or three central bones of

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* "Über die Vermehrung des Os centrale in Carpus und Tarsus des Axolotls," von R. WIEDERSHEIM, 'Morphol. Jahrb.,' vol. 6, 1880, p 581, Taf. xxx.

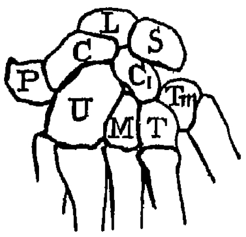
† The unciform bone in *Thylacinus* appears to be formed by union of two elements.

‡ "Über die Extremitäten einer jungen *Hatteria*," von Dr. FRANZ BAYER, in Tabor, 'Wien, Akad, Sitzber,' vol. 90 (Abth. 1), 1885.

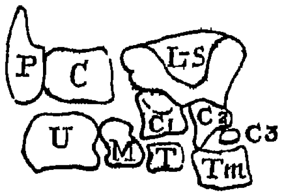
§ 'American Naturalist,' February, 1885, p. 195.

‖ "Quadrumana," 'TODD, Cyclopædia Anat.,' vol. 4, part 1, 1852, p. 203.

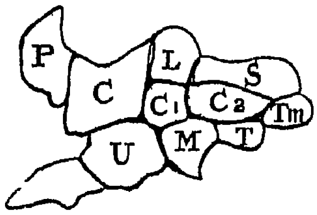
Amphibians, *Hatteria*, and certain Chelonians must indicate a closer genetic relation between *Theriodesmus* and some of the lower Vertebrata.



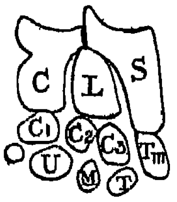
Carpus of *Cheiromys*



Carpus of *Theriodesmus*



Carpus of *Hatteria.*



Carpus of *Axolotl*

The Metacarpus.

The metacarpus consists of five stout bones, which are deep from back to front at their junction with the carpus, and wide from side to side at their distal ends. The transverse width over the proximal end of the metacarpus is 2·6 centims. These bones successively augment in length from the first to the fourth, but the fifth is shorter than the second. As a whole the metacarpus is very Mammalian, being like that of the Otter, and several of the smaller Carnivora. But the plan of the metacarpus is also interesting from its resemblance to the metatarsus in *Protorosaurus* and the Scaphosaurians.

The first metacarpal is 1 centim. long, the second 2·1 centims. long, the third measures 2·7 centims., the fourth 2·8 centims., while the length of the fifth metacarpal is reduced to 2 centims. The middle three bones have their distal ends strong, and are flattened superiorly. Their relative length is characteristic of the Carnivora. The several bones have their sides concave, but the concavity is most marked on the external side. The superior surface is convex from side to side, with the oblique convexity most marked on the outer side in the outer digits, and on the inner side in the inner digits.

The depth of the proximal end of the first metacarpal is 6 millims.; its width at the proximal end is 2 millims., and rather less at the distal end. The proximal articulation is truncated and flat. The distal articulation is well rounded from above downward.

The second metacarpal is between 5 and 6 millims. wide proximally, contracting in the middle to 4 millims., and expanding distally to a width of nearly 8 millims. The distal articulation is nearly straight transversely, and the convexity from above downward is less distinctly shown. The lateral border, which faces the third metacarpal, is more concave than that which faces the second. Above the distal condyle there is a slight transverse depression, but all the bones want the supracondylar grooves which are commonly found among Mammals.

The third metacarpal is 5 millims. wide proximally, it soon contracts to 4 millims., and expands distally to 9 millims. The outer corner of the distal end is obliquely truncated, and is not articular, so that neither in this digit nor the next is the proximal end of the first phalange as wide as the metacarpal with which it articulates.

The fourth metacarpal is 5 millims. wide proximally, contracts to 4 millims., and expands distally to 9 millims.; but, though these transverse measurements are the same as in the third, the configuration of the bone is different, because the distal widening is here gradual from the proximal third of the bone, while the third metacarpal widens rapidly near the distal end. A short ridge descends obliquely from the inner angle of the proximal articulation.

The fifth metacarpal bone has its proximal articular end directed inward It is 6 millims. wide, the distal end is about equally wide, and in the middle the shaft contracts to between 3 and 4 millims. The inner lateral border is nearly straight, except that there is a marked concavity below the articulation, which may result from the inflexion of the inner proximal angle, such as is seen in the fourth metacarpal Distally there is some appearance of a ridge on the superior inner border of the bone.

The Digits

The digits are imperfectly preserved. In each the first phalange is large and strong, but the other phalangeal bones are short. In the fifth digit there are three phalanges, and the fourth has the same number, but the third appears to have had four phalanges. In the second digit only two phalanges are preserved, and the first has but one preserved and a second indicated.

In the first digit the first phalange is 8 millims. long. It is wide at the proximal end, where the articulation is concave from side to side. It appears to have a well-developed anterior end, with a rounded articulation, margined superiorly by a slight groove. In close contact with this surface is a small hemispherical ossification which appears to represent a second phalange.

In the second digit the stout first phalange is 12 millims. long. It is 7 millims. wide proximally and 5 millims. distally, but contracts rapidly below the proximal articulation. The second phalange is similar in form, but smaller, being 7 millims. long. Its distal extremity appears to have been articular, but there is no trace of a third phalange, which may have been preserved in the counterpart slab.

In the third digit the first phalange is relatively long and slender. It measures 13 millims. in length, is 8 millims. wide proximally, and about half as wide distally. The second phalange is hardly more than 3 millims. long; and the third is nearly 7 millims long. It has a good trochlear distal end, and beyond it is an indication of a fourth bone, but there is no evidence to show whether it was a complete phalange.

In the fourth digit the first phalange is 15 millims. long, so that the first phalangeal bones follow the same law of progressive elongation as the metacarpals. The bone is rather stouter than the others, being less contracted distally. The second phalange is about 3 millims. long, but more than 5 millims. wide. Anterior to this is a curved mass of most irregular form, with a striated surface, which I regard as being the extremity of the digit, but the absence of definition of the joints leads me to believe that the original bones had been lost, and replaced, as among some of the lower Vertebrata, by fibro-cartilage imperfectly ossified, and that this tissue, with the attached ligaments, has been preserved, but only defines the third phalange, which is not terminal.

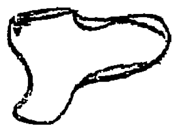
The fifth digit is well preserved. The first phalange is 1 centim long, the second 5 millims. long, and the third is a slightly curved claw phalange 5 millims. long. These three bones steadily diminish in size.

The characters in this hand, which are new, are first evidence of an augmentation in the number of phalanges in the middle digits. But, although the three phalanges in such digits are singularly constant in the Mammalian class, the existence of so remarkable a departure from the usual rule as is found in the Cetacea, will show that the increased number is not inconsistent with the Mammalian plan, and not inconsistent with the number being different in nearly allied genera. Still the increased number in *Theriodesmus* is suggestive of a lower Vertebrate type, just as is the possible replacement of the extremity of the fourth digit. The form of the metacarpals, enlarged distally and flattened superiorly, is suggestive of the Marsupial *Thylacinus*, while the shortness of the phalanges and the character of their articular ends is not unlike the condition in *Echidna*. Still, neither Monotremes nor Marsupials make any approach to carpus in character. But the *Echidna* has the distal end of the ulna and radius simpler than in most unguiculate terrestrial Mammalia.

Tibia and Fibula.

The right tibia and fibula are parallel bones, imperfectly displayed, and imperfect proximally. Little more is known of the fibula than that it equalled the tibia in length; it was apparently more slender, similarly straight, was contracted at the distal end, and slightly expanded proximally, where it is 13 millims. wide.

The tibia is a stout strong bone, somewhat disfigured by crushing. The postero-exterior side is exposed in which the bone faces towards the fibula. At the distal end it is fully 13 millims. wide; it there thickens from front to back so as to make a convex outline towards the articulation. The middle of this convexity is inclined towards the inner side of the bone, up which it runs as a narrow, rounded, marginal ridge, which separates the convex anterior surface from the flattened and sub-concave posterior surface. In the middle third the width of the shaft is 1 centim., but the width increases proximally to 1·7 centim. at the fracture, partly by the great increase in strength of the convex lateral ridge, and partly by expansion towards the fibula. The distal articular end of the bone is inclined obliquely backward; the surface, partially exposed, is as deep as wide, is gently convex, and not smooth, but slightly irregular, as though it were cartilaginous. Below it, separated by a distance of a centimetre, is a bone which from its form might well be the distal epiphysis. It is 11 millims. wide and 8 millims. deep on the inner side, where its contour is vertical, with the distal surface notched out so as to give the bone a descending talon, which



apparently would have fitted on to an astragalus No affinities can be inferred from these bones, which are little more than 10 centims. long.

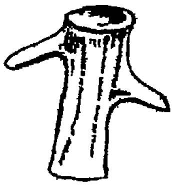
Caudal Vertebra.

An impression of a caudal vertebra exhibits the under side, transverse processes, anterior articular end, and some indication of the small depressed neural arch.

The centrum, as displayed, is 14 millims long, with the anterior articular end of the centrum transversely ovate, 6 millims. wide, and about 4 millims deep. The articular margin is rounded, and there is a marked concavity occupying the larger part of the articular surface.

The ventral aspect is very slightly constricted transversely, with blunt, longitudinal, lateral ridges margining the base, which is flattened, slightly concave between the ridges, and gently concave in length. The transverse processes are thin, compressed from above downward, about half a centimetre long, directed obliquely outward and backward They are given off from the middle of the height of the side of the centrum, near to its anterior end, the sharp anterior ridge of the process rising immediately behind the articular face, though the process on the left side is carried further back than that on the right side. The transverse width over the processes is 12 millims.

The neural arch is only indicated by a slight trace of the prezygapophyses, which shows that the neural canal was very depressed. No affinities can be found in an isolated caudal vertebra like this, though its characters are Mammalian.



Ventral aspect, candal vertebra.

Conclusion.

From the foregoing description it is manifest that *Theriodesmus* is a primitive Mammal of a generalised type, which diverges much less from existing orders than might have been expected, seeing that no limb bones have hitherto been known from the secondary rocks, with the exception of the small humerus and femur from the Stonesfield slate.[*] With that type this fossil has nothing in common. If the humerus only had been found in this South African animal, it would have been regarded as indicating a Carnivorous type, probably Marsupial. The ulna and radius in their proximal ends and general character correspond with Carnivora and Lemuroids, but in their distal ends are more like certain Rodents and the Monotreme *Echidna.* This I take to indicate that there may have been no supination, and that the distal extremities of the bones acquired their modification after the Carnivorous characteristic had been developed Some caution may be needed in drawing inferences from the carpus, because the bones are not all in natural articulation. But the presence of the bones of the central series seems beyond question The prevalence of the central ossification in the Quadrumana, Lemuroidea, and certain Rodents points to a collateral affinity with those groups, the former two of which have obvious points of contact with Carnivora. The absence of the centrale in the Monotremata and Marsupialia suggests that, if *Theriodesmus* is not Placental, it has no close kinship with any surviving type of Marsupial, while the fact that as many as three central bones are present, tends to show that it is of a more ancient stock, even if it should prove to be an offshoot from the Lemuroid division of Mammalia. The close general rememblance of the carpus, but for the central bones, to the carpus of a Carnivore is suggestive of relations to the Carnivora as well. The metacarpus is that of a Carnivore like the Otter, simplified in details in a way found among Marsupials The phalanges are short as in terrestrial Chelonians, and have the superior surfaces but little modified, indicating a plantigrade movement, or very little motion between the phalanges of the digits.

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[*] 'Geol. Soc Quart. Journ,' vol. 35, 1879, p 456.

Hence I conclude that this fossil cannot be placed in any defined order of existing Mammals. It would appear to belong to that group or sub-class which Professor COPE has named Bunotheria, but not to any order of it which has been indicated. For, while it is like the Bunotheria in being on a lower grade than the existing Placental Mammals, it is of higher type than the Creodonta, and the structures described suggest that higher Placental types may have diverged from the order of which it is the first indication

The question arises whether *Tritilodon,* founded on the anterior part of the skull, described by Sir R. OWEN, from the Trias of Thaba-chou, Basutoland, South Africa, may be the skull of the same animal? I regard the two animals as having no close family relation. The skull, as judged by its dentition, is a Bunotheroid Rodent; while this fore-limb is that of a Bunotheroid type which lies between the Lemurs and Carnivora; yet the distal ends of ulna and radius do not indicate a typical Carnivorous dentition. These remains are probably but the beginnings of a Mammalian fauna which the South African rocks may be expected to yield to systematic exploration, which will show other evidences of Reptilian inheritance. It is in the Mammalia that many characters of extinct Amphibian and Reptilian ordinal groups must be sought for.

Explanation of Plate.

PLATE 26.

Fig 1 A slab showing the right fore-limb and some bones of the hind-limb of a Mammal from South Africa (*Theriodesmus phylarchus*). Natural size.

a.	Humerus
b.	Ulna.
c.	Radius
d.	Scapho-lunar bone.
e.	Cuneiform and *f.* pisiform.
g, h, i.	Centralia.
k, l, m, n.	Trapezoid, trapezium, magnum, and unciform.
o, I., II., III, IV, V.	The metacarpus
p, I, II, III., IV., V.	The first phalange in the five digits.
q, I, II, III, IV, V.	Second phalange.
r, III., IV, V	Third phalange.
s, III, ?	Fourth phalange
t.	Mass at the extremity of the fourth digit, drawn enlarged in fig. 2
v, w.	Tibia and fibula.
x.	Distal epiphysis of tibia.

Fig. 2. The fourth digit enlarged three times, showing the first, second, and third phalanges, *p, q, r*, and a mass *t* extending distally. The processes which extend from *r* are regarded as ossified ligaments, and it is possible that the part of the digit from *r* downward may have been lost and replaced by fibro-cartilage.

VI. *The Post-Embryonic Development of* Julus terrestris

By F G. HEATHCOTE, *M.A , Fellow of the Cambridge Philosophical Society.*
Communicated by ADAM SEDGWICK, *F.R.S*

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[PLATES 27-30]

IN a former paper I traced the development of *Julus terrestris* from the ovum within the ovary up to the bursting of the shell and the liberation of the young animal on the twelfth day. In the present paper I propose to take the different organs one by one, and to describe their development. This different way of treating the subject seemed to me to be the best . firstly, on account of the difficulty of describing a long and complicated development like that undergone by *Julus* in its larval life by dividing the history of its growth into periods of time, and, secondly, on account of the nature of the work which has hitherto been done upon this subject

The two most important works bearing on the subject of my paper are those of NEWPORT (13)* and METSCHNIKOFF (12). The former has observed the general development of *Julus terrestris*, and has given us a most accurate and full description of the external features of the young animals at various stages, from the time of hatching almost up to the adult condition.

METSCHNIKOFF carried on his observations principally on *Strongylosoma Guerinii*, but also investigated the development of other forms, amongst them a species of *Julus*—*Julus Moreletti*—the development of which, he says, agrees almost completely with that of *Strongylosoma.*

NEWPORT'S observations with regard to the external features of the development leave me but little to say; nevertheless, there is one matter which requires a few words. According to NEWPORT, the third body-segment is apodous, as is the case in the adult; while in METSCHNIKOFF'S figure of the young *Strongylosoma* it is the second segment which is without a pair of legs. The question as to which segment is apodous is not so easy to settle as it appears at first sight, and it is very hard to come to a satisfactory conclusion. That there is a great difference between the larval and adult conditions may be seen from figs. 1 and 2 (Plate 27).

Fig. 1 is a drawing of the anterior region of the hexapodous larva, with the ventral

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* The numbers within brackets refer to the List of Literature at the end of the paper.

side uppermost (magnified about 150 diameters). The first pair of legs, *p* 1, seem to belong to the broad neckpiece, 1 *br*, the lateral ends of which do not meet ventrally. The ends of the second ring meet ventrally, forming a complete ring round the body, and it seems as if this segment had no pair of legs. The second pair, *p* 2, seem to belong to the next ring, 3 *br*, and the third pair to the next ring, 4 *br*.

Now, in fig. 2, which is a slightly magnified drawing of the ventral side of the anterior region of an adult *Julus*, the ends of the *third* ring, 3 *br*, meet, and it appears as if this segment, and not the second, as in the larva, had no leg-pair. It might be expected that the nerve cord would afford some help in settling the question as to which segments the pairs of legs belong to, by showing the ganglia from which the leg-pairs are supplied, but in the young animal it is impossible to get a satisfactory longitudinal section showing all the ganglia at once, and in the adult the anterior ganglia are fused into an indistinguishable mass. On the whole, I am inclined, from a consideration of my sections, to think that the first segment of the body is really the apodous one, and that its ganglion fuses early with that in front of it, and that in the course of development the leg-pairs become shifted forward, so as to bring about the difference between the larval and the adult condition which I have shown in figs. 1 and 2.

If this view is correct, it would seem probable that, comparing the appendages with those of Insects, the first body segment (apodous) is equivalent to that which in Insects bears the second pair of maxillæ, while the first pair of legs in *Chilognatha* is equivalent to the first pair of legs in Insects.

The appearance of the ends of the antennæ at an early stage is very peculiar, the antennæ terminating in two long and thick projections, as shown in Plate 27, fig. 4, *pr*. The *Julus* from which the drawing was taken had three pairs of fully-developed legs, but the legs had not yet appeared on the fifth and sixth body segments.

The Cœlom and Generative Organ.

In a paper on the development of the *Chilognatha* (12) METSCHNIKOFF describes the formation of the mesoblastic segments and their protrusion into the legs, and also the separation of the part within the legs from that in the body. He states that in *Strongylosoma* both parts break up into heaps of cells and form muscles.

In *Julus terrestris*, however, this is not the case, and in spite of the difficulties of investigating the final behaviour of the somites in this particular animal, I have succeeded in tracing the alterations they undergo, and have satisfied myself that their development strongly resembles that of the somites in *Peripatus* as regards essentials, though this similarity does not hold in respect of the less important details.

In a former paper (7) I described the arrangement of the greater part of the mesoblast in two longitudinal bands, and the formation of the mesoblastic segments.

Shortly before the young animal is hatched a cavity appears in each mesoblastic segment, as shown in fig. 5, *c s*, thus forming a kind of vesicle. There are two of these vesicles in each body segment, one on each side, and they are joined by a thin sheet of mesoblast covering the nerve-cord. The mesoblastic cells are easily distinguished from the adjoining epiblast cells by their appearance. They are of a more irregular shape and their protoplasm is clearer, while their nucleus is larger and is very distinct. When the epiblast begins to be thrust out at a certain point to form the first rudiment of an appendage, the vesicle protrudes also, and as the appendage becomes larger, part of the vesicle or somite projects within its cavity. This part is eventually constricted off, as shown in fig 6, *s.s*, and *cr*, *s*, so that we have a vesicle-like part of a somite in the appendage and a vesicle-like part of a somite within the body on either side, connected by a thin sheet of mesoblast passing above the nerve-cord to its fellow on the other side of the body

The cavity within the part of the somite which has remained within the body, and also the cavity in the part within the appendage, constitute, in my opinion, the cœlom, and are equivalent to the similar structures in *Peripatus* and other animals. The part within the body I shall call the somatic part of the cœlom, and that within the legs the crural part of the cœlom.

Leaving for the present the consideration of the fate of the somites of particular segments, I will describe the process which occurs in the greater number of segments in the body. The part of the somite which remains in the appendage loses its cavity, and remains for some time as a mere mass of mesoblast cells within the hollow of the appendage. As the limb grows larger and longer, the mesoblast cells within it lengthen out, change their shape and character, and become the muscles of the leg; this agrees completely with the description of METSCHNIKOFF. The part within the body, however, has a different fate The vesicles become larger and thinner-walled, and gradually alter their position, moving along the sheet of mesoblast covering the nerve-cord, so as to approach one another. This is shown in fig. 8, *s.s.* As the animal becomes adult they meet above the nerve-cord and fuse with one another, so as to form one continuous tube. A stage where the fusion is almost complete is shown in figs 9, 10. This tube is the generative organ, which in *Julus* is placed between the nerve-cord and the gut The structure of the generative tube when just formed is shown in Plates 27, 28, figs. 10, 17, where it consists of a single layer of long cells, with elongated nuclei.

Transverse sections through the generative tube of a female *Julus* of a rather greater age than the one from which fig. 10 was taken, show us the origin of the ova. Figs. 17, 18, 19, 20, 21 show parts of the wall of the generative tube. The cells of which it is composed are much elongated, and have oval nuclei; their protoplasm is very clear, and in all respects they resemble the cells of the cœlomic vesicle. In parts of the generative tube the cells undergo a change. They increase in number, as shown in figs. 18, 19, and some of them attain a larger size. Some of these are destined to become the young ova, while others divide more quickly and form the cells of the follicle which envelop the ova.

A more advanced stage of this process is shown in fig. 20, where some of these cells have increased in size, while others are being divided off from the wall of the ovary In fig 21, an ovum has attained a considerable size, while some of the cells have already formed a follicular envelope round it (F c)

In his paper on the generative organs and the egg in the *Annulosa* (11) LUBBOCK pointed out a difference between the ovaries of Myriapods and of Insects; namely, that in Insects like *Coccus* the follicle projected *from* the ovary, while in Myriapods the follicle projects *into* the ovary, the difference being, in his own words "If, therefore, we consider the ovary as consisting of an outer membrane and an inner epithelial layer, it would appear that while the egg in the Myriapods arises between these two layers, in the Insects it originates on the inner side of both." In the development of the ovary in *Julus*, however, we see that, as in fig. 17, the ovary at the stage when the ova first appear does not consist of two distinct layers between which the ova are formed, but that at certain points the follicle cells, as well as the young ova, are formed from cells budded off from those which compose the single-layered wall of the ovary. Therefore, the distinction pointed out by LUBBOCK, though no doubt valuable as an anatomical character, does not seem to receive much light from embryology.

It will be seen from the foregoing account that the cœlomic spaces have nothing to do with the body-cavity, or vascular system of *Julus*. The body-cavity is a series of spaces contained between the gut and the body-wall. In the earlier stages of development it was represented (see paper 7) by a network formed of mesoblast cells, derived directly from the endoderm and containing the yolk-spherules within its meshes. The yolk-spherules are absorbed in the course of development, and the body-cavity of the adult results from the joining together of the spaces already present in the spongy network. The body-cavity of *Julus* is therefore a pseudocœle, like that of *Peripatus*. I shall deal with the vascular system later on.

I will now consider the behaviour of particular somites The first pair is that of the antennæ. The part within the appendage gives rise to muscles as happens in other somites. The somatic part breaks up, I believe, and also furnishes muscles, but I have not been able to follow its fate satisfactorily, at any rate it disappears at an early stage. The somites of the mandibles also disappear and are lost; but those of the third pair [the third pair of appendages afterwards becomes the plate beneath the mouth, the deutomalæ of PACKARD (14)] give rise to the salivary glands and thus show a resemblance to *Peripatus*, where the salivary gland arises from the lateral part of the third somite. The details of this process are shown in figs. 11, 12, 13, 14. Fig. 12 is a drawing from a longitudinal section through a young *Julus* just after leaving the shell. The third and fourth segments are shown. The fourth segment shows part of the mass of cells within the rudimentary limb and the somatic part of the somite separated from it. In the third segment there are a few cells representing the crural part of the somite, while the somatic part presents a different appearance to that of the fourth segment. It is much more elongated, and the cells composing it have somewhat altered their character, showing a more regular outline than the cells of the other somites at the same stage Fig 13 is a transverse section through the third segment of a young *Julus* of a rather more advanced age. The rudiment of the salivary gland has lengthened since the first stage, and is beginning to curve in the direction of its future course, so that the section has cut it nearly transversely The cells within the limb are the cells remaining from the crural portion of the somite, and are not yet altered to form muscles. In fig. 14 the salivary gland has a more definite shape, while the mesoblast cells of the crural part have assumed the appearance of muscle-cells, and have already separated into several bundles of muscles which have been cut at different angles The opening to the exterior is not yet formed. Fig. 11 shows a later stage, where the salivary gland has acquired an opening to the exterior. It is a longitudinal section through the head cut so as to show the three first appendages; the third being the plate resulting from the fusion of the third pair. The salivary gland on each side opens at the base of the labial plate (*deutomalæ*) by an opening formed after the gland has attained a considerable size.

In the posterior region of the body, that is, in the so-called segments, there are as METSCHNIKOFF stated (12) two somites to each body-ring This is shown in fig. 16, which is a drawing from a section cut longitudinally through a young *Julus*, with three pairs of legs and two double pairs just forming, each double pair being still enveloped in a single sac. The section has cut through the fifth segment through the base of the double pair of appendages rather obliquely, so that one somite, that of the posterior of the double pair, is better shown than that of the more anterior. The crural division of the somite is a mass of cells which has lost its cavity, but is still connected with the somatic part An earlier stage in the same process is shown in fig 15—a transverse section through a segment which is just forming—the section has been cut rather obliquely so that the thickness of the epidermis is exaggerated. The double nerve cord is just differentiated from the epidermis, and is cut through so as to divide a ganglion. The thickening of the mesoblast forming the somite, has also been cut through, but as yet there is no cavity in it. The two somites are joined by a thin sheet of mesoblast covering the nerve cord. The only point in which the section shows a difference from sections through the early stages of the formation of the first segments is in the presence of a layer of hypodermic matrix outside the epiblastic layer, from which the nerve-cord is formed. The characteristic appearance of the cells of the different layers is as marked as in the case of the earlier stages of the development.

Comparing the development of the cœlom with that of the cœlom of *Peripatus*, it is clear that while the resemblance of the general plan is very conspicuous, the details differ considerably. In the posterior part of the body of *Julus*, that is behind the third body-segment, we have a part of the somite in the limbs, and a part in the body. The body-part passes towards the top of the nerve-cord, not to the dorsal part of the body as in *Peripatus* (16).

Thus far the resemblance is striking. But the part of the somite within the limbs, which in *Peripatus* forms the nephridium and the vesicle into which the nephridium opens, undergoes a totally different change in *Julus* The cells alter their character, and furnish the muscles of the limbs In the development of the salivary gland, too, there is a difference between that in *Julus* and that in *Peripatus*. The body part of the somite in *Peripatus* furnishes the musculature of the pharynx, and the part in the appendage forms the salivary gland and the vesicle into which it opens. In *Julus*, as we have seen, it is the body part of the somite which furnishes the salivary gland, while the limb part provides the muscles which move the plate representing the fused pair of appendages. In describing the formation of the salivary gland I mentioned the changed character of the cells of the somatic part of the somite at a very early stage, and I regard this early change as indicating that the process does not represent the gradual alteration of the somatic part of the somite into a tubular salivary gland, but rather a sudden loss of the character of the somite, and the assumption of the character of a different organ. In other words, the difference from the other somites observed at so early a period, indicates an abbreviation of development, some intermediate stage having dropped out.

One of the most interesting points about the development of the somites is the fact that the so-called double segments have two mesoblastic segments each. As is well known, Newport held that each double segment represented two single segments of an earlier stage in the phylogeny, which had become fused, and retained traces of their original condition. Later on, Balfour suggested that the double segments might represent single segments which had developed a second pair of limbs, and had altered the nerve-system and other organs to suit them. He was followed in this suggestion by Packard (14), and later by Grassi (5). It seems to me that this view is contradicted by the facts just mentioned, inasmuch as the segmentation of the mesoblast is one of the most primitive processes in the development, and affords us the best guide to the consideration of the segmentation of the adult

The presence of two nerve-ganglia to each double segment also favours the belief that each of the latter represents two perfect segments, but I should not be inclined to consider this of itself as sufficiently strong evidence, since the nerve-system undergoes so much modification, in the course of development, that one might easily suppose that a stage where one ganglion to each double segment had existed had dropped out of the development. I cannot, however, suppose this in the case of the mesoblastic segments. The external skeleton of the animal does not exactly coincide with the mesoblastic segmentation, and I hold that the surest guide in considering the segmentation of the adult is the early mesoblastic segmentation.

The Nervous System.

The first appearance of the brain and ventral nerve-cord was described shortly in a former paper (7) and has also been described for *Strongylosoma Guerinii* by METSCHNIKOFF (12). There are, however, one or two points in the later development which deserve notice. The most interesting of these is the appearance of a pair of cerebral grooves resembling those in *Peripatus* These grooves make their appearance about the time when the young animal leaves the shell. At first they are only shallow depressions, but soon they grow deeper, and eventually have the appearance of two vesicles just within the substance of the brain and communicating with the exterior by narrow openings. In fig 28 the vesicle appears closed, but a few sections further back in the series the opening was visible These cerebral grooves do not persist, but a few days later when the three leg-pairs of the larva are complete, they become obliterated and disappear entirely, leaving, as far as I can see, no trace of their former existence. The chief alterations in the shape of the brain in its development are due to the outgrowth of the optic and antennal lobes.

When the ventral nerve-cord is first formed it consists, as is already known, of two cords with ganglionic enlargements on them, and united by a thin median sheet. When the nerve-cord is entirely separated from the epiblast, a species of cavity appears in the ganglia. A ganglion at this stage, with this cavity, is shown in Plate 29, fig. 30, which was drawn from a longitudinal vertical section of a *Julus* which had just left the shell. The section had cut through the middle of the fourth ganglion of the body, and this is the ganglion shown in the figure. The cavity is also shown in fig. 29, *cav. gl*, where it is gradually becoming obliterated.

The presence of these cavities is not a permanent feature, as they become obliterated when the two cords unite to form a single cord. About the second day after hatching, the nerve-cord—that is, all of it which is as yet developed—undergoes a considerable change, and as new segments are formed their nerve-cord in turn undergoes a like process. The paired ganglia approach one another in the middle line, and join so that the space between them is gradually obliterated, at the same time, the cavities in the ganglia, of which I have spoken, gradually disappear. The effect of all this is to change the shape of the transverse section of the ventral nervous system, from that of two cords united by a thin median sheet, to that of a single stout cord enlarged at the ganglia and showing but a slight trace of its former double character. At the same time the fibrous part of the cord begins to make its appearance. It occurs first at the median dorsal line and increases as the development proceeds till the cord assumes its characteristic appearance, as shown in fig. 23.

Fig. 29 shows the process of the junction of the cords. It is drawn from a transverse section through the third segment of a young *Julus* on the first day after hatching. The cavities in the ganglia are almost obliterated, but are still present, while the only trace of the separation between the cords consists of a small slit-like space in the centre of the ventral nerve-system. The fibrous portion of the cord is distinctly marked off from the surrounding ganglionic part, but is still small. Two nerves are passing off from the ventro-lateral parts of the ganglia.

The cavities which appear in the ganglia have not, in my opinion, anything to do with the cerebral grooves They differ from the latter in not possessing at any period a connection with the exterior. They exist only for a short time, and disappear completely I am altogether unable to suggest any explanation of them, and am uncertain whether they have any ancestral meaning or not. Possibly a further study of Myriapod embryology would throw some light upon them. The cerebral grooves, which are not an uncommon feature of arthropod development, have a great resemblance to those in *Peripatus*. It is possible that they may supply the want of aeration to the mass of cerebral tissue, as they appear just after hatching and disappear as soon as the tracheal invaginations begin to be formed.

The Tracheæ.

A pit-like invagination is formed just behind and a little externally to the bases of each pair of appendages One of these tracheal invaginations is shown in fig. 22, *T I* This invagination, the walls of which are thick and are composed of cells like those of the epidermis, gradually becomes deeper and increases in size so as to form a kind of vesicle within the body, close to the nerve-cord (figs 23, *T I.*; 8, *T I*) This vesicle changes its form, giving off two short thick diverticula, one into the space below the nerve-cord, where it nearly meets its fellow of the opposite side, and the other dorsal-wards, parallel to the body-wall. This is shown in fig. 23. The cells composing these two diverticula break up, alter their arrangement, and form the tracheal tubes. The main part of the vesicle near the leg remains as the tracheal pit, while the diverticulum beneath the nerve-cord breaks up to form the mass of tracheal tubes which occupies that position in the adult. The other diverticulum forms the main tubes, which run dorsal-wards, and give off twigs to the different organs.

In the double segments there are two pairs of these tracheal invaginations; an invagination close to each leg.

The Stink Glands (glardulæ odoriferæ).

In METSCHNIKOFF's paper on the development of the *Chilognatha* (12) he describes the appearance of a paired organ of which he was unable to discover the fate. These organs, which appear at a stage when three pairs of limbs are present, are the first pair of stink glands. They make their appearance as invaginations of the ectoderm in the side of the body in the fifth segment (fig. 24). The invagination increases in size and swells out till it assumes the vesicle-like shape which it attains in the adult Late in the development a muscular wall is added. The adult structure of these glands has been described by VOGES and other writers, especially WEBER (18) There is a slight peculiarity about the first pair of these glands formed, which is worth mention. They are placed in a slightly different position to those formed later, inasmuch as they are situated rather more dorsally. The difference is slight but perceptible There is only one pair to each double segment, and they do not occur in any of the single (anterior) segments Fig 25 is part of a section through the first pair of these glands at an advanced stage, when the external coat is already added

The Heart and Fat-body.

The mesoblast cells remaining in the yolk, and described in a former paper (7), as derived from the hypoblast, give rise to the heart and fat-body. Soon after the young animal leaves the shell a number of mesoblast cells are collected in the dorsal region of the animal near the future position of the heart. These cells are of irregular amœba-like form, and their processes anastomize so as to form a network, as shown in figs 31, 32, 33. The tube of the heart is formed by the coming together of the meshes of this network, as shown in fig 33, while other processes of the cells give rise to the various muscles of the heart The ostia are spaces left open in the formation of the tube and are not subsequent perforations. In each double segment there are two constrictions formed, as shown in fig. 35, *os* · these are the lips of the ostia in course of formation, and are not, as supposed by NEWPORT, a junction of two separate chambers. The blood corpuscles are also formed by these mesoblast cells

The fat-bodies are formed by the same mesoblastic cells, which when the yolk is completely absorbed are present as a sort of network occupying the position of the future fat-bodies (fig. 34, *F b.*). Later in the development there is a copious secretion of oil globules in the cells composing the network, and they finally assume the character of the fat-body cells, as shown in figs 36, 37, *F.b.* I believe that all the cells of the fat-body have this character, and I have not observed two different kinds of cells in the adult fat-body, the only difference being in the amount of oil globules secreted, some cells being almost free from them.

As the heart of the adult *Julus* has never been fully described, it is necessary to give a somewhat more detailed account of its structure than I have done for most of the adult organs.

The heart in the adult is situated dorsally between the hypodermic matrix and the digestive tube. There are two pairs of ostia in each segment, situated nearly dorsally (fig. 36, *os*). These ostia are originally spaces left in the tube during development. The shape of each ostium is shown in fig. 38, and it will be seen that the ostia resemble the second modification described by GRABER in his paper on the Insect heart (3). The lips of the ostia which project into the tube of the heart are formed by four peculiarly-shaped muscle-cells, shown in Plate 30, fig. 40, which evidently control the operations of the ostium. The arteries (fig. 37) are situated more ventrally than the ostia, and there are two pairs to each segment. They are placed nearer the centre of the segment than are the ostia. NEWPORT describes them as given off close to the ostia. These arteries lead directly into the spaces of the fat-body. The tube of the adult heart consists of three coats (fig. 39), corresponding to the "Intima," "Muskelschicht," and "Adventitia," of GRABER (3) Of these coats the internal ("Intima") is not nucleated, being secreted by the cells of the middle coat ("Muskelschicht") early in development. The middle of the three coats ("Muskelschicht") is a well-developed muscular structure. The striæ are well marked and the nuclei easily seen. The arrangement of the muscles is worth notice The fibres are circular and are disposed in bands; a narrow band alternating with a broad one This coat, which is derived directly from the cells of which the heart was first composed, is the principal structure of the circulatory apparatus. The external coat ("Adventitia") is formed of connective tissue, and is continued over the arteries. It does not appear till late in the development. It is shown in figs 37, 39.

It will be seen that this account of the heart of *Julus* agrees rather with GRABER's and LANDOIS' description of the Insect heart than with that of WEISMANN (19). NEWPORT describes the heart of Myriapods generally as consisting of three coats, but gives no account of the heart of *Julus* in particular

The heart is suspended by thin muscle fibres, which are attached to the hypodermic matrix layer There are also muscle fibres which are attached to the fat-body and probably correspond to the aliform muscles of the Insect heart The cavity in which the adult heart of *Julus* is enclosed is partially cut off from the rest of the body-cavity by a pericardial membrane, formed from the same network of cells which gives rise to the heart and which is continuous with the fat-bodies. This is shown in figs. 36, 39.

The Eye.

The formation of the eye begins on the fourth day of larval life as described by NEWPORT, and continues until the animal is adult. A single ocellus appears first, and the rest are added one by one till the full number is reached The process of development is the same in the case of each eye-spot. A deposition of pigment granules of a dark red-brown colour takes place within a thickened mass, which has been formed by a multiplication of the cells of the hypodermis, and this secretion of pigment is accompanied by a separation from one another of certain cells within the mass. The result of this process is the formation of a vesicle bounded by a mass of dark pigment. The cells composing the external wall of this vesicle, *i.e.*, the part of the vesicle nearest the surface of the body, give rise to the lens which fuses with the chitin of the exoskeleton, and the same cells continually add layers to the lens till it assumes its full size. They are then, as far as I have been able to follow their fate, absorbed, their nuclei disappearing altogether, and their substance furnishing the last layer of chitin to the lens.

It is possible that these cells may still exist in the adult eye, but I have been unable to see them The difficulties of decolorising and preserving render it very hard to say definitely that such cells are not present. The nuclei, which are very distinct in the earlier stages, become fainter and fainter as the later stages are reached till, in the adult, they fade away altogether.

Figs 44, A, B, C, show the earliest stage I have been able to obtain. They are taken from transverse sections through the head of a young *Julus* about four days after hatching; and owing to the small amount of pigment present at this stage, it was unnecessary to decolorise They show three consecutive sections through the eye at the time of the beginning of the first ocellus The hypodermis is thickened, and forms a mass round the first pigment spot The pigment is disposed round the small hollow space which I have called the vesicle The nuclei are rather large and stain deeply.

Figs 45, 46, show a later stage in the development of the same eye-spot. The eye, when viewed from the exterior, had the appearance shown in fig. 50, the spot *oc*, 2, being a new eye-spot just forming. Soon after the stage shown in these figures a capsular membrane is formed round the ocellus by the mesoblast cells in the body. The appearance of this capsule will be best understood by a reference to fig. 53, which is a section rather obliquely through a fairly-developed eye-spot. The section has cut so far to one side of the middle line that it has missed the lens altogether, and instead of cutting the cavity of the vesicle, has cut along the side of its wall.

Figs 49, 51, show that the front wall of the vesicle has become thinner, and is composed of a single layer of cells, which, as I have before mentioned, will secrete the lens. Fig 52 shows a further stage. The cells forming the back and sides of the vesicle have become longer and are beginning to assume their final shape; while the cells of the front wall have become very thin and are adapted to the shape of the increasing lens to which they make additions. In the course of the further development to the perfect eye-spot, the principal changes are connected with the increasing size of the lens, which becomes so large as almost completely to fill the space which was originally the hollow of the vesicle. The cells of the back and sides of the vesicle lengthen and assume their final shape. The thin front-wall cells lose their nuclei, as I have already mentioned; the back and sides of the vesicle remaining continuous with the hypodermis.

Before the period at which the eye begins to be formed, the hypodermis consists of a layer of cells one cell thick. The cells themselves are oblong, and are arranged so that their long axes lie parallel to the surface. The chitinous exoskeleton is secreted at the outer edge of these cells. Just before the first eye-spot makes its appearance the hypodermic cells alter their shape and become larger and of a more round form. They then begin to divide and multiply, so as to form the mass in which the first formation of the eye begins.

The cells forming the walls of the vesicle are all of a roundish, but somewhat irregular, shape. As soon as the vesicle is formed, while it is as yet quite small, the cells forming the back and sides begin to elongate, and at the same time a junction takes place between them and the ganglionic cells of the brain. Fig 55 shows two ganglion cells and two cells of the back wall of the vesicle joined together. I have not made out the exact period when this connection takes place, but just before the appearance of the vesicle there is no such connection—the separation of the brain from the epidermis being complete.

The cells forming the back and side walls of the vesicle elongate as the latter increases in size, and pigment is deposited at the surface of the upper (*i.e.*, the part nearest the interior of the vesicle) two-thirds of each cell. This is shown in fig 57, which is a drawing of a single cell from the back wall of an ocellus The pigment is all confined to the external two-thirds of the cell, the part round the nucleus being clear. The end pointing towards the surface forms the rod ("Stabchen" of GRENACHER) which is therefore terminal, not axial, thus agreeing with PATTEN's expectations (15). I have been unable to make out the fringed ends of the rods described by GRENACHER (6). I find, in a transverse section cutting an adult ocellus in a plane parallel to the surface, that I get the same appearance as GRENACHER described; in fact, his figure would serve for an exact representation of my section, but I believe this appearance, which I do not get in similar sections through earlier stages, is due to the action of reagents At no stage of the development could I see anything like an axial fibre in the retinal cells of the ocelli.

The cells of the exterior wall become flat rather than round, and their nuclei become very faint during the latter part of their development.

The capsule forming the covering of the ocelli is a cellular membrane formed by the mesoblast cells of the body-cavity which have been mentioned before. They begin to form the capsule at a very early period of the vesicle stage.

Just before the formation of the capsule a number of small irregular amœba-like cells make their appearance within the eye mass, and among the cells forming the lateral and internal walls of the vesicle (figs 45, 46, 47, 48, *pg.c.*, *mes c*). These eventually develop into cells like those called pigment cells by GRENACHER. I believe them to be descended from the irregular amœba-like mesoblast cells, present within the body-cavity, for the following reasons.—No such cells are present within the eye mass before the period just mentioned as that at which they make their appearance Just before they make their appearance, the mesoblast cells are present in considerable numbers close to the ocelli, and some of them are in the act of dividing rapidly, the division resulting in the presence of very small irregular-shaped cells resembling those afterwards found within the walls of the vesicle All sizes are found, from the parent mesoblast cells to the small cells just mentioned (fig 47). Now, the only other cells from which the pigment cells could have originated are those of the walls of the vesicle, and if this were the case, I should expect to find some traces of division, and some intermediate-sized cells between the long-shaped large cells of the vesicle, and the very small irregularly-shaped cells which I have called the pigment cells. If I am justified in my belief, that these small cells which appear in the walls of the ocelli are descendants of the mesoblast cells of the body-cavity which have wandered into the ocellus, they are evidently intrusive pigment cells, like those described by KINGSLEY in his development of the eye of *Crangon* (8), and by LANKESTER and BOURNE for the eye of *Scorpio* (9).

In fig. 46 the continuations of the cells of the internal wall of the vesicle have collected so as to form a nerve which joins the brain (fig 46, *n, oc*). This nerve pierces the capsule as described by GRENACHER. I do not think this the place for a detailed account of the adult eye, a subject which I hope to take up at a future time

The formation of the simple eye-spots of *Julus* as just described exhibits a curious type of development, and one which, so far as I know, is unlike anything which has yet been investigated It is clear that the mass of the ommateum is of exclusively hypodermic origin, while the capsule is mesoblastic, and, if I am right in the view expressed some lines further back, the pigment cells are also mesoblastic. The cells forming the front wall of the vesicle and furnishing the lens must be regarded, in my opinion, as having kept in a great measure their hypodermic function, the clear lens being in its structure and mode of formation exactly similar to the ordinary chitinous exoskeleton which covers the rest of the body at this stage. I do not, therefore, regard the front wall of the vesicle as representing the vitreous body cells, but as ordinary hypodermic matrix. The internal and lateral walls of the vesicle are cells which have become changed and have lost their hypodermic function, while they have acquired or retained the epidermic function of retinal cells. The mode of development seems to me to indicate that the eye-spot of *Julus* is not the most primitive type of eye, but that it has been evolved from a more primitive form of eye, the traces of which have been retained. The distinct vesicle formed as the first starting point seems to me to be such a primitive feature If my views as to the pigment cells are correct, the first formation of pigment by the cells of the vesicle and the later intrusion of the pigment cells from the mesoblast indicates that the present exochromic eye of *Julus* was derived from an earlier autochromic eye. The ordinary hypodermic cells of the matrix layer are themselves capable of forming pigment, as is shown in fig. 58, which is a section through the hypodermis of a young though adult *Julus*. The pigment is here formed round the surface of the cells exactly as in the earlier stages of the vesicle. From this I conclude that the pigment cells of the ocellus in *Julus* have a function beyond the mere production of pigment. They probably serve to pack the other cells of the vesicle, like the intra-neural cells of the Scorpion eye, as described by LANKESTER (9).

The development of the eye-spots of *Julus* from a vesicle agrees with PATTEN'S belief that the simple eye of Myriapods has been developed from a vesicle invaginated from the ectoderm, as shown in his diagram [fig. 143 of his paper (15)].

The front wall of the vesicle, however, which should according to him be the vitreous layer, is clearly the corneal hypodermis. The original hypodermis present before the formation of the eye (according to PATTEN the external of the three layers), is represented by the external chitin of the exoskeleton formed by it, and now fused with the external wall of the vesicle which now represents the corneal hypodermis.

General Conclusions.

The previous part of this paper contains the chief facts of the development which I have succeeded in obtaining, and I will now consider whether they have any bearing on the more general questions of the phylogeny of the Myriapoda. One of the most important of. these questions in view of the recent researches on *Peripatus* is whether the development of *Julus terrestris* offers any points of resemblance to that of this animal. That it does so, I think, is hardly to be denied. The formation of the mesoblastic somites and the origin of the generative tube are strikingly similar. The behaviour of the crural part of the somite is, however, different; the difference being apparently due to the disappearance of the segmental organs. The formation of the salivary gland, while it resembles that of *Peripatus* in being derived from the somite, yet differs completely in the fact that it is formed from the somatic part of the somite.

The formation of the nerve-cord does not in my opinion show any very striking resemblance to that of *Peripatus.* The points in which it agrees are only general resemblances, such as might occur in almost any Tracheate. The development of the eye does afford some ground for believing it to be derived from an eye like that of *Peripatus*, inasmuch as it is formed from a vesicle, but this resemblance is only a general one, and the retinal elements are not, as in *Peripatus,* derived directly from the brain. The heart and pericardium show a striking similarity to those of *Peripatus* in their development as spaces in the mesoderm separate from the cœlomic spaces of the somites. This also is probably a feature common to many Arthropods. The presence of the cerebral grooves is another *Peripatus*-like feature of the development which is also a general point and common to other Tracheates. Thus we see that while there are many similar features in the two developments they are for the most part of a general character, and are at the same time essential features which would be likely to occur in many Tracheata, assuming that the latter are descended from a *Peripatus*-like ancestor.

One part of the development of *Julus terrestris* seems to me to have an interest when considered in its relation to the recent investigations of Mr. SCUDDER on the Carboniferous Myriapods (17). In a former paper (7) I drew attention to the early form of the nervous system, and showed that the two cords which formed its principal part were widely separated; and in the present paper I have shown that in the further course of development the cords came together, and fused, so as to form a single cord. A reference to figs. 1 and 23 of this paper, and to fig. 34 of my former paper (7), will show that this tendency to concentration is shared by the limbs, and also by the whole ventral surface of the body. Now, in SCUDDER's paper on the structure and affinities of the Carboniferous Myriapods of the genus *Euphoberia* (17) he points out features which correspond exactly with this embryonic condition of *Julus.* He describes the ventral plates of *Euphoberia* as occupying the whole ventral surface of the body, and the legs of each pair as placed at some distance from one another, so as to have a clear space between them. It must be remembered that the approximation of the legs and the reduction of the ventral region is a distinguishing character of the existing Diplopoda.

A most interesting question relating to the phylogenetic history of the Myriapods is the matter of the so-called double segments Were they originally two distinct segments, or were they single segments which have acquired a second pair of limbs? NEWPORT supported the first view; while subsequent writers, especially BALFOUR (though he only suggested it, not considering the evidence sufficient to come to a definite conclusion) and PACKARD, advocated the second. The latter writer puts the evidence in favour of this view very clearly, so I will quote his words (14):—"The phenomenon of two pairs of limbs to a segment, so unique in Tracheata, may be explained by reference to the Phyllopoda among the Branchiata. The parallel is quite exact The larvæ in both groups have but a single pair of appendages to a segment; the acquisition of a second pair in the Diplopods is clearly enough a secondary character, and perhaps necessary in locomotion in a cylindrical body with no sterna" He adds in a note·—"It is plain that, as BALFOUR suggests ('Comparative Embryology,' p. 324), the double segments have not originated from a fusion of two primitively distinct segments. There is, however, a misconception as to the nature of the 'double segments.' They are not so, in fact The scutes are single, undivided, but the ventral region is alone imperfectly double, bearing two pairs of appendages, just as single segments of Apodidæ may bear from two to six appendages; the differentiation is confined to the ventral limb-bearing region and limbs alone; the dorsal part of the segment does not share in the process"

The results of the present paper, however, show that the double character of the segments is a much more essential one than is assumed by the acceptance of the above view. The circulatory system, the tracheal system, the nerve-cord, and above all the mesoblastic segmentation, all show this duplication; and the only parts of the double segments which are single are the broad plate covering the dorsal and lateral parts of the body, and the stink glands, which, as I have shown, are invaginated in the dorsal plates during development. Looking at the palæontology of the subject, we see that even the dorsal part of the body-ring ("scute" of PACKARD) shows distinct traces of a division in the most ancient classes of fossil Myriapods The Archipolypoda, an order including the families of Archiclesmidæ, Euphoberidæ, and Archijulidæ, show this peculiarity (ZITTEL's 'Handbuch der Palæontologie').

NEWPORT (13) spoke of the double segments as resulting from the fusion of two originally distinct segments, but it seems to me that it is more correct to consider each part of the so-called double segments as a segment complete in itself but joined to its fellow by the fusion of two dorsal plates, a circumstance probably due to the process of concentration which we see has taken place in the ventral region of the body, with the result that relations which were originally *Euphoberia* are changed to those obtaining in the adult *Julus.*

I fully recognise the difficulty of drawing any definite conclusions as to the phylogeny of a class from the embryology of a single form; at the same time the results of my investigations seem to me to indicate that the Chilopods and Diplopods branched off from some common ancestor at some period not very long before the appearance of the Archipolypoda, and that both are remotely descended from some *Peripatus*-like stock.

My investigations, the results of which are included in this paper, were begun in 1882, and have been entirely carried on in the Morphological Laboratory at Cambridge.

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DESCRIPTION OF PLATES 27–30 *

Lettering used throughout the figures.

Al.	Aliform muscle.
An.	Antenna.
Art.	Artery.
b r.	Body ring.
brn.	Brain
C	Cavity.
Cap	Capsule.
Cer.gr.	Cerebral groove.
Ch.	Chitinous exoskeleton.
Cor.	Cornea.
Cr.s.	Crural part of somite.
Deut.m.	Deutomalæ.
Ep.	Epidermis.
Ex.	Chitinous covering and hypodermis.
Ex.c.	External coat.
F.b.	Fat-body.
F.w.	Front wall.
F.c.	Follicle cells.
G.	Gut.
Gl.	Ganglion.
H	Heart.
Hyp.m.	Hypodermic matrix.
In.	Invagination.
Int.	Internal coat
L.	Leg.
Ln.	Lens.
M.	Mesoblast.
Mes.c.	Mesoblast cells.
Musc.	Muscle.
M.w.	Muscular wall.
Malp.T.	Malpighian tube.
N.cl	Nerve cell.
N.S.	Nerve system.
N.	Nucleus.
N.wk.	Network.
O.	Ovum.
Oc.	Ocellus.

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* The first four figures were drawn for me, under the microscope, by Mr. H. CHAPMAN, and I am indebted to him for the great care and patience with which he fulfilled his difficult task. The remaining figures were drawn by myself, under ZEISS' camera lucida, and are, unless stated to the contrary in the description of the figure, actual representations of my sections

Os.	Ostium
P	Pair of legs.
Pr	Projection.
Pg	Pigment
Pg c	Pigment cells.
Pro.m.	Protomalæ.
Percd.	Pericardium.
S.	Somite.
SS.	Somatic part of somite
Sal gl.	Salivary gland.
Sec.c.	Secreting cells.
Seg	Division of segment.
St.gl.	Stink glands.
Sus.m.	Suspensory muscle.
T I	Tracheal invagination.
Up L.	Upper lip.
Ves.	Vesicle.
V.bl.s	Ventral blood space
V.N C	Ventral nerve cord.
W ov	Wall of ovary.
Y S.	Yolk spheres.

PLATE 27.

Fig 1. Drawing of a young *Julus,* late in the stage where three pairs of legs are present Slightly magnified. *An.* Antenna *Oc.* Ocelli. 1 *br.* First body ring. 2 *br.* Second body ring 3 *br* Third body ring. 4 *br.* Fourth body ring. *P.* 1, 2, 3. First, second, and third pairs of limbs.

Fig. 2. Drawing of an adult *Julus,* showing the first three pairs of legs. *An.* Antenna. 1 *br.* 2 *br.* 3 *br.* 4 *br.* First, second, third, and fourth body rings.

Fig. 3. Drawing of the ventral side of the head of a just-hatched *Julus,* showing the relative position of the mouth parts. Magnified about 150 times *An.* Antennæ. *Pro.m.* The mandibles or protomalæ of PACKARD *Deut m.* The maxillæ or deutomalæ of PACKARD (afterwards form a broad plate).

Fig. 4. Drawing of the antenna of a young *Julus,* in the same stage as Fig. 1. *pr.* The projecting spikes at end of antenna.

Fig. 5. (ZEISS F. *Oc.* 2). Drawn from a longitudinal vertical section of the 10th day *Julus.* The section cuts the 3rd segment. The mesoblastic segment has a cavity within it · The cœlom. *Ep.* Epiblast. *S.* The mesoblastic somite. *C.S* The cavity within the somite or cœlom.

Fig. 6. (REICHERT, $\frac{1}{15}$ *homog* *Oc.* 1). A slightly later stage. The somite has divided into two parts. *SS.* Somatic part of somite. *Cr.s.* Crural part of somite. *SS.* Somatic part of somite. *Ep.* Epiblast. *YS.* Yolk spherules.

Fig. 7. (ZEISS F. *Oc.* 2). A slightly older stage. The crural part of the somite has lost its cavity. The somatic part is slightly pushed out of place by the invagination of the tracheal sac. *M.* The thin sheet of mesoblast uniting the two somites. *N.C.* Nerve cord. *SS.* Somatic part of somite. *Ep.* Epiblast. *C.S.* Crural part. *T.I.* Tracheal invagination.

Fig 8. Magnified 450 diameters. A later stage than the foregoing. The somatic part of the cœlom is passing upwards towards the top of the nerve cord. *T I.* Tracheal invagination. *SS.* Somatic part of somite *M.* Mesoblast uniting somites across the nerve cord *F.N S.* Fibrous part of nerve cord *G N.S.* Ganglionic part of nerve cord.

Fig. 9. The two somatic parts have met above the nerve cord to form the generative tube. A section through the whole animal, magnified about 250 diameters. *H* Heart *F b.* Fat-body. *N C.* Nerve cord. *G.* Gut. *SS.* Somites

Fig. 10 Part of the same section as the last. Magnified 450 diameters. *C.SS.* Cavity of somite. *F N.S* Fibrous part of nerve cord. *G.N.S.* Ganglionic part of nerve cord.

Fig. 11. ($\frac{2}{3}$-in Beck *Oc.* 5 Zeiss). A longitudinal section through the head of a young animal, late in the stage where three pairs of legs are present, to show the salivary gland. *Up L.* Upper lip *brn.* Brain. *Sal gl.* Salivary gland. *Pro.m.* Protomalæ. *Deut m.* Deutomalæ. *P.* 1. First pair of legs

Fig. 12 450 diameters. Longitudinal vertical through the 3rd and 4th segments, showing the first development of the salivary gland. *SS.* 4. Somatic part of somite of 4th segment. *Cr.s* Crural part of somite. *SS.* 3. Somatic part of 3rd somite.

Fig. 13. Magnified 250 diameters. Part of a transverse section cutting the somite of the 3rd pair of appendages (later the deutomalæ). *Sal.gl.* Salivary gland. *Cr.s.* Crural part of the somite. *Ep* Epidermis.

Fig. 14. 450 diameters. Part of a longitudinal section cutting the same segment. *Sal.gl.* Salivary gland. *Musc.* Muscles of limb. *Deut m.* One of the deutomalæ.

PLATE 28.

Fig. 15. 500 diameters. Ventral half of a transverse section through a freshly developing segment (double segment). This section was cut rather obliquely, so that the epidermis seems rather thicker than it would otherwise. *Ep.* Epidermis. *Hyp.m.* Hypodermic matrix. *M.S.* Mesoblastic somite. *Gl.N.C.* Ganglion of nerve-cord. *M.* Thin layer of mesoblast uniting ganglia.

Fig. 16. Part of a longitudinal section through a young animal late in the three-legged stage, cutting the bases of the 4th and 5th pairs of legs (the legs of the first double segment). *L.* 4. One of the 4th pair of legs. *L.* 5. One of the 5th pair. *SS.L.* 5. Somatic part of the somites of the 4th and 5th pair. *Cr.s.* 4. Crural part of somite of 4th pair.

Fig 17. Magnified 250 diameters. Part of a transverse section through a young *Julus* with perfect ovary *N.C* Nerve-cord. *V.bl.sin* Part of the ventral blood sinus. *W ov.* Wall of ovary. *Ov.* Young ovum. *F c* Follicle cells.

Fig. 18. Part of the wall of the ovary of the same *Julus*, magnified 450 diameters. *W.ov.* Wall of the ovary. *C.ov.* Cells divided off from the cells of the cell-wall.

Fig. 19. 450 diameters. Another part of same ovary, cells divided off from wall of ovary rather bigger. *W ov.* Wall of ovary. *Ov.* Young ovum *C ov.* Cells divided off from wall of ovary.

Fig. 20. Another part of same ovary. Same magnification. Letters as before.

Fig. 21. Another part of same ovary. Same magnification. One cell has reached a considerable size, and will become a young ovum; others have surrounded it, and will form the follicle.

Fig. 22. Magnified 450 diameters. Part of a transverse section through a *Julus* with three pairs of legs, to show the first invagination of tracheæ. *SS* Somatic part of somite. *T.I.* Tracheal invagination. *L.* Limb. *N.C.* Nerve-cord.

Fig 23. Half of a transverse section through a late hexapodous stage *G* Gut. *Malp T.* Malpighian tube. *SS* Somatic part of somite. *Tr.I.* Tracheal invagination. *L* Leg. *Y.S.* Yolk spherule.

Fig. 24. First invagination of stink gland. The section is a longitudinal one through part of the 7th segment when first formed. *St.gl.in.* Invagination of epidermis to form stink gland. *Musc.* Muscles.

Fig. 25. Part of a longitudinal section showing a later stage in the formation of the stink gland. Magnified 250 times. *Hyp m.* Hypodermic matrix. *M.St.gl* Mouth of stink gland. *St.gl.* Stink gland. *Ext.c.st gl.* External coat of stink gland.

Fig. 26. Part of a transverse section through a later stink gland, to show structure. Magnified 450 times. *Ext.c.st.gl* External coat of stink gland. *Sec.c.* Secreting cells.

Fig. 27. Part of a longitudinal section through the head region of a just-hatched *Julus*, to show brain. 250 diameters. *Cer.gr.* Cerebral groove *brn.* Brain. *Hyp.m* Hypodermic matrix. *Gl.* Ganglia. *G.* Gut. *V.N.C.* Ventral nerve-cord.

Fig. 28. Transverse section through head of *Julus* of same age as the last, to show brain. 250 diameters. *Hyp.m.* Hypodermic matrix. *Cer.gr.* Cerebral groove. *G.* Gut. *F.br.* Fibrous part of the brain.

PLATE 29.

Fig. 29. Transverse section through animal a little later than fig. 28 250 diameters. *G.* Gut. *M.* Mesoblastic covering of gut. *Sp.* Small cavity remaining after the two ganglia have approached and fused. *Cav.gl.* Cavity in ganglion. *Y.S.* Yolk spheres. *Cr.s.* Crural part of somite still remaining. *tr.i* Tracheal invagination.

Fig. 30 Section through 3rd ganglion of ventral cord, soon after first formation. *Cav gl* Cavity in ganglion. *M.* Mesoblastic covering of ganglion.

Fig 31 (Zeiss F. *Oc.* 2.) Dorsal part of a transverse section through a young *Julus* shortly after hatching, showing the network of mesoblastic cells from which both the heart and the fat-body are formed. *Ch.* Chitinous exoskeleton. *Hyp m.* Hypodermic matrix. *N wk.* Network of mesoblast cells.

Fig 32. A highly magnified (Zeiss L water immersion, *Oc.* 2) part of the network. *Y S.* Yolk spherules. *C.* Cells. *N.* Nucleus.

Fig 33. (Zeiss D. *Oc.* 2.) A more advanced stage than fig. 31. *Ch* Chitinous exoskeleton. *Hyp.m.* Hypodermic matrix. *Susp.m* Fibre forming suspensory muscle of heart. *N.wk.* Cells forming network. *C.ht.* Cavity of heart.

Fig. 34 Later stage. The chitinous exoskeleton has been rather torn away from the hypodermic layer in the act of cutting. *Y.S.* Yolk spheres. *C.ht.* Cavity of heart. *Percd.* Pericardium. *Musc* Muscles. *F.b.* Part of the forming network.

Fig. 35. ($\frac{1}{15}$ *hom. im.* Reichert.) Part of a longitudinal section through a forming segment in posterior region of heart. *Ch.* Chitinous exoskeleton. *Ht.* Heart. *Os.* Ostium forming *Wg.* Wall of gut. *Ex.* Exoskeleton of segment.

Fig. 36. (Zeiss D. *Oc.* 2) Adult *Julus.* Part of a longitudinal section to show heart. *Ch.* Exoskeleton. *Hyp.m* Hypodermic matrix. *Seg.* Division between segments. *F.b.* Fat-bodies. *Ht.* Heart. *Percd* Pericardium. *Os.* Ostium.

Fig. 37. (Zeiss D. *Oc.* 2) Part of a longitudinal horizontal section through an adult *Julus* to show artery. The external coat of the heart is continued over the artery. *F.b.* Fat-body. *O.gl.* Oil globule. *Art.* Artery. *Ext.c.* External coat of heart.

Fig. 38. Longitudinal section through a heart nearly formed, in a *Julus* with seven pairs of legs. *Ht.* Cavity of heart. *Os.* Ostium.

Fig. 39. Transverse section through nearly formed heart. *Ext.c.* Forming external coat. *M.w.* Muscular wall of heart. *Int.* Intima. *Percd.* Pericardium. *Al.mus.* Fibre which represents aliform muscle in Insect heart.

PLATE 30.

Fig 40 ($\frac{1}{15}$ REICHERT *Oc.* 2.) Transverse section through adult heart, showing ostium. *Os.* Ostium. *Mus.* Muscles of ostium.

Fig. 41. ($\frac{1}{15}$ REICHERT *Oc.* 2.) Part of a section through a forming heart, to show the formation of the external coat and suspensory muscle.

Fig 42. ($\frac{1}{15}$ REICHERT *Oc.* 2) Part of a longitudinal section through an adult heart, to show the arrangement of muscles in alternate broad and narrow bands. *Int.* Internal coat. *B.mus.* Bands of muscles. *Sus m.* Attachment of a suspensory muscle.

Fig. 43. (REICHERT $\frac{1}{15}$ *Oc.* 2.) Structure of external coat of adult heart; from a longitudinal section.

Fig. 44. A, B, C. Three consecutive sections through the beginning of the first eye-spot. The hypodermis is slightly thickened round the beginning ocellus. *Pg.* Pigment. *Oc.* Beginning of ocellus.

Fig. 45. Section through further advanced ocellus. *Mes.c.* Mesoblast cell in body cavity. *Cap.c* Cell of forming connective tissue capsule. *Pg.c.* Pigment cells *Ves.* Vesicle.

Fig. 46. About same age as last. *P.c.* Pigment cells. *No.c* Nerve from ocellus. *Ves.* Vesicle.

Fig. 47. Further advanced ocellus. *Ves.* Vesicle. *F.w.ves.* Front of vesicle. *Oc.* Ocellus.

Fig. 48. Section through advanced ocellus, and cutting a more complete ocellus obliquely. *Oc.* Advanced ocellus, cut obliquely. *F.w.ves.* Front wall of vesicle. *Ves.* Vesicle. *Hyp.* Hypodermis. *P.g.* Pigment cells.

Fig. 49. Further advanced ocellus. *Ch.* Exoskeleton. *Hyp.m.* Hypodermis. *Ves* Vesicle. *Pg.c.* Pigment cell.

Fig. 50. 150 diameters. Head of young *Julus.* *Oc.* 1. Advanced ocellus. *Oc.* 2. Beginning ocellus.

Fig. 51. *Cor.* Thickened chitin, the beginning of the cornea. *F.w.v.* Front wall of vesicle from which the corneal lens is increased. *B.w.v.* Back wall of vesicle. *Cap.* Capsule.

Fig. 52. (REICHERT $\frac{1}{15}$ *homogen. Oc.* 1.) The lens is beginning to be formed. *B.w.v.* Back wall of vesicle. *Cap.* Capsular membrane. *Hyp.* Hypodermis. *Ln.* Lens.

Fig. 53. Section through advanced ocellus. The section is taken through the side of the ocellus, and not through the middle line. *Ch.* Chitinous exoskeleton. *F.w.v.* Front wall of vesicle. *Cap.* Capsule. *B.w.v.* Back wall of vesicle.

Fig. 54. Pigment cell inside ocellus, to show size relative to surrounding cells. About 700 diameters.

Fig. 55. (Reichert $\frac{1}{15}$ *homogen. Oc.* 1) Early stage of ocellus, to show junction between the cells of the vesicle and the nerve-cells. *Hyp.* Hypodermis. *Ves.* Vesicle. *Con.p.* Process connecting the nerve-cell and the vesicle cell. *N.C.* Nerve-cord.

Fig. 56. Single cell from nearly adult ocellus.

Fig. 57. Cells from retina of nearly adult ocellus.

Fig. 58. Part of transverse section through adult exoskeleton and hypodermis *Ch.* Exoskeleton. *Hyp.m.* Hypodermic matrix. *Pg.* Pigmented part of hypodermic matrix cells

VII. *On Parts of the Skeleton of* Meiolania platyceps (Ow.)

By Sir Richard Owen, *K.C.B., F.R.S., &c.*

Received March 29,—Read April 21, 1887

[Plates 31–37.]

Since my last communication to the Royal Society (March 15, 1886) of the characters of some fossil bones of a *Meiolania* from Lord Howe's Island, I have been favoured with the opportunity of inspecting a second and richer series of remains of the same extinct genus of Reptile from the same island and formation.

These fossils have been liberally transmitted by Charles Wilkinson, Esq., F.G.S., F.L.S., Government Geologist of the Department of Mines, Sydney, to the Geological Department of the British Museum of Natural History, and have been confided by the Keeper, Dr. Woodward, F.R.S., for their development from the matrix, to Mr Richard Hall, Assistant Mason in that Department, whose name deserves to be recorded for the patient devotion and admirable skill with which he has brought to light the manifold and complex evidences of osseous structure, especially of the cranial and some vertebral parts of the petrified skeletons of the present singular genus of extinct Reptile.

The subjects of Plates 31–34 give four views of the skull of *Meiolania platyceps.* Plate 31 gives a side view; Plate 32 represents the base of the skull, with three attached vertebræ; Plate 33 shows the outer plate of the cranial wall, with the horn-cores, Plate 34, the back view. All the figures are of the natural size.

With the exception of the outer plate of the cranial wall, the subject of Plate 31 includes the rest of the skull, of which the facial division shows the orbits, *o*, the outer nostril, *n*, and both upper, *m*, and lower, *g*, jaw-bones. The auditory chamber has its external osseous aperture, 1 inch in diameter, at the side of the cranium, 2½ inches behind the orbit. In Plate 32, at the under part of the tract, between the par-, *b*, and ex-, *c*, occipitals, are the pair of long and slender auditory ossicles, *e*, slightly expanding where they enter the matrix which blocks up the *meatus auditorius internus*, *v*.

The side view of this skull (Plate 31) shows an almost vertical tract of bone, extending from the auditory, *p*, to the optic, *o*, foramen. It descends from the upper surface of the cranium with a slight bend outward, ending below in a sharp margin,

27.4.88

until it expands into the sub-auditory enlargement, developing the joint for the mandibular condyle. The above-described vertical side-plate include the post-frontal, *w*, and mastoid, *x*, above, the malar, *m*, and zygomatic, *z*, bones below. These are distinct and separate bones in the *Chelonia* (Tortoise) and most existing Reptiles, but are here confluent with each other and contiguous parts of the skull

Turning to the base of the skull (Plate 32), the lower border of the single occipital condyle, *a*, appears anterior to the joint with the atlas, *va*. In advance of this, a pair of ridges diverge and expand to coalesce with the broader basisphenoid, *f*, forming on each side, behind, a thick angular prominence. In advance of these, the sides of the coalesced basi- and presphenoids extend outwards, expanding into a convex roof of the auditory outer chamber, and coalescing with the articular process, *g*, for the mandibular joint. The hind border of the bony palate (Plate 32), *h*, completes below the transverse slit-shaped single inner or hinder nostril, *h'*, the roof or sides of which are formed by the basi- and presphenoids; the backward position of this aperture and concomitant extent of the bony palate bespeak the Saurian affinity of this extinct toothless Reptile. The cornua, *l*, *l*, of the os hyoides have been preserved in the present skull, each 3 inches in length, one-third of an inch in thickness at their obtuse inner or mesial ends, here adherent to the basisphenoid; they slightly taper to the outer obtuse end, also adherent by matrix to the paroccipital, *b*.

Returning to the facial portion of the present skull (Plate 31), the orbital contour, *o*, is subtriangular, the angles rounded off, and the apex directed forward; the longitudinal diameter of the visual aperture is 40 mm., the vertical one, 35 mm.

The inner or mesial wall of the orbit is entire, and is separated by a wide interspace of the broad facial part of the skull of *Meiolania* from the mesial bony wall of the opposite side. They do not communicate, as in *Chelonia*, with the nasal chamber; this extends backward with walls unbroken by such communication. About 25 mm. extent of the malo-maxillary tract, *l*, *m*, leads from the orbit to the single outer nostril, *n*. This aperture is 40 mm. in transverse, 20 mm. in vertical diameter; the fore-margin of the bony septum is concave, it rises about 10 mm. behind the lower boundary of the nostril to coalesce with the roof of the nasal passages. In Chelonian Reptiles the sutures persist which indicate the six several facial bones which enter into the frame of the anterior or external nostrils.* From the nostril the upper jaw descends obliquely backward to terminate in its trenchant toothless border. This border shows a small median notch. It extends a little in advance of the corresponding border of the under jaw, *q*. The interspace left by the fossil between these borders may be interpreted as having been occupied by the part of the trenchant horny sheath forming the beak of the Megalanian Reptiles.

Of the mandible, *q*, the length of each ramus from the angle to the symphysis, in a straight line, is 120 mm.; the greatest depth of the ramus is 38 mm., this is a little behind the plane of the orbit. The angle of the jaw, *r*, extends 8 mm. behind the glenoid cavity, in form of a subvertical ridge inclined backward and inward. The outer roughish surface of the mandible bulges slightly beneath the fore part of the broad zygoma. There is no marginal extension of the mandibular ramus meriting the name of "coronoid process," and no indication of sutures of the usual constituents of the lower jaw in the Reptilian class.

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* See Cuvier, 'Leçons d'Anatomie Comparée,' 2e éd , 1837, vol. 2, p. 501.

On the upper surface of the facial part of the skull, a subcircular vacuity, due to fracture, about 30 mm behind the upper border of the nostril, indicates the position of a broken-off core of the nasal horn.

The bony palate (Plate 32), *h*, 3 inches in length, 2 inches in breadth, is concave, has a medial longitudinal ridge, and a pair of lateral lower ones it terminates behind in a vertically narrow, transversely extended, post-narial aperture, *h*, 30 mm. in extent. On each side of this aperture the bony palate is continued into the lateral expansion of the basi-pre-sphenoid, *f*, *g*. To these are attached, by matrix, the hyoid cornua, *i*, *i*.

The length of the skull from the super-occipital border to the outer nostril, the boundary of which is the foremost part of the cranium, is 7 inches. the upper surface of the skull thus forms an equilateral triangle.

A second cranial specimen (Plates 33 and 34) supplies what is wanting in the one above described. It includes the hind portion of the skull. The single occipital condyle, *a*, has suffered only a slight abrasion of the surface. The super-occipital ridge, *d*, extends from the occipital foramen, *w*, upwards and backwards, ending in a sharp border behind, but expanding as it ascends to support the backward continuation of the outer wall of the cranium (Plates 31 and 34), *x*, which terminates in an obtuse free margin, describing an arch, the supports or wings of which coalesce with the outer osseous expansions developing the processes affording the articular surfaces, *u*, *u*, for the mandibular condyles.

The supra-cranial wall includes the cores of the low hindmost pair, *c*, of horns. The larger cores, *b*, rise in advance of and exterior to these; the length of this core, in the subject of Plates 33 and 34, is 2 inches. The cores of the antero-lateral horns, *a*, are low, small, obtusely ridged processes, the longest basal diameter not exceeding 1 inch. The outer, horn-supporting, wall of the skull (Plate 34), *x*, *x*, is here preserved for an extent forwards of 5½ inches, where the rest of the skull has been broken away; the breadth of the preserved calvarium is 7 inches. In advance of the larger horn-cores is a pair of low convexities, due to thickening of the bony plate, each about 2 inches in diameter. The sides of this portion of skull-plate bend down at a right angle, (Plate 34), *x*, *x*, with a slight partial prominence, to the part where a thick bony extension of the inner surface contributes to support the glenoid articular surface, *u*, for the condyle of the lower jaw.

The external auditory aperture (Plate 31, *p*), is about 1 inch from the lower border of this part of the outer wall of the cranium and 1½ inch below the base of the anterior horn-core, its vertical diameter is 1¼ inch, its transverse diameter is 1 inch. A wide, irregular "meatus" open below (Plate 32), *p′*, extends for 2 inches before attaining the opening (*meatus internus*) at the side of the inner or proper cranial wall of the acoustic chamber. In these wide passages lay the slender, long *ossicula auditus* preserved in the preceding cranial subject. In the subject of Plate 34 are seen the strong outward extensions of the confluent exoccipitals and alisphenoids, 2–5, which expand and coalesce with the parts of the outer cranial wall supporting the first and second pairs of horn-cores.

To the skull, the subject of Plate 32, are cemented by matrix the three anterior vertebræ, *va*, *vb*, *vc*, the atlantal ring is completed below by a hypapophysis confluent with the neural arch, developing a low obtuse transverse process on each side, and a broader depressed plate representing the neural spine. The true "centrum" of the atlas has coalesced with that of the second or "axis" vertebra, *vb*, as the "odontoid process." The body of a third cervical vertebra, *vc*, retains the proximal end of the rib of one side, showing a well-developed "head" and "tubercle," partially dislocated from the vertebra The body of this segment of the spine is flattened beneath and expands as it extends backward, where it presents a pair of short thick angles. A strong transverse process extends from the side of the centrum and presents an articular surface for the head of a rib.

The separate vertebræ transmitted with the cranial fossils above described exemplify modifications in the different regions of the column, but are not in numbers sufficient to yield that (numerical) character. The size concurs, however, with their colour and petrified state, as fossils, in yielding evidence of their relation to the skull of *Meiolania.* The coalescence of the neural arch and centrum repeats the evidence of individual maturity given by the attached cervical vertebræ; the separate ones present also three well-marked modifications of the terminal joints of the centrum.*

I may also premise that, in the existing Crocodiles, the centrum of the axis vertebra is flat in front, convex behind; that an anterior sacral vertebra is concave at the fore part, flat at the hind part of the centrum; a posterior sacral vertebra is flat at the fore part, concave at the hind part of the centrum; also, that the first or foremost caudal vertebra is convex at both ends of the centrum, and that the bodies of the dorso-lumbar vertebra are concave in front, convex behind. In the extinct Crocodiles of Secondary Periods below the Cretaceous Series, both articular surfaces of the centrum in the trunk-vertebræ may be slightly concave; in one Oolitic genus the fore end of the centrum is convex, the hind end concave, whence the generic name, *Strepto-spondylus*, of this fossil form. This "opisthocœlian" articulation is also shown in the cervical and anterior dorsal vertebræ of the gigantic extinct *Cetiosaurus.* Allied modifications may be seen in corresponding vertebræ of *Dinosauria* exhibited in the Geological Department of the British Museum of Natural History.

[illegible] which gives the subjects of figures 1, 2, 3, Plate 35, has the characters [illegible] probably from the fore part of the dorsal region The trans-[illegible] and par-apophyses) have shallow terminal articular surfaces

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[illegible] the spinal column of several existing Chelonians for the "head" and "tubercle" of the pair of ribs which had been thereto articulated. The centrum is "pro-cœlian"; the "cup" (*c*, fig. 1) with its margin sharply defined; the "ball" (*c′*, fig 3) is hemispheric and correspondingly well-defined.

The parapophyses (*p*), short and thick, are developed from the lower and fore part of the side of the centrum. Each diapophysis (*d*) is continued with a downward inclination from the base of the neurapophysis, *n*. Both these "transverse processes" have a small shallow semicircular articular cavity, for the "head" and "tubercle" respectively, of a thoracic rib. The centrum expands to form the anterior cup and contiguous parapophyses; the under surface shows posteriorly a low transverse protuberance, *t*, fig 2, ending in lateral, low, smooth convexities, divided by a narrow groove from the lower border of the articular ball

With the centrum the neural arch has coalesced, as in a warm-blooded Mammal, without trace of early suture. The diapophysis, *d*, short and thick, has a truncate shallow articular surface for the "tubercle" of a rib, looking downward and slightly backward. The articular concavity, *p*, on the parapophysis for the "head" of the rib, similarly shallow, is smaller, circular, and looks outward and slightly backward. The presence of both par- and diapophyses, with concomitant bifurcate proximal ends of ribs, is a character ascribed to *Dinosauria* as well as to the Reptilian orders *Anomodontia*, *Ichthyopterygia*, and *Crocodilia.*[*]

The neurapophysis, *n*, sends forward the prezygapophyses, figs. 1, 2, *z*, with their flat, articular surfaces directed upward and slightly inward, the postzygapophyses, figs. 2, 3, *z′*, with opposite aspects, occupy half of the vertical extension, representing a short, broad neural spine, which terminates in a mere ridge expanding behind into a low notched tuberosity. The neural canal, *nc*, indicates by its expanse a large myelon and concomitant strong muscularity. The following are dimensions of this vertebra :—

	Inches	Lines.
Extreme breadth	2	9
„ length . .	2	4
„ height . .	3	0
Breadth of articular cup .	1	5
Height of „ „ . .	1	0

Of the rich series of fossils the subject of the present paper, no vertebra, or fragment of vertebra, affords an indication of having been modified in relation to a Chelonian carapace or plastron.

A biconvex vertebra, answering to the foremost caudal in a Crocodile, is represented by the centrum only, fig. 4, Plate 35, the fractured bases of neurapophyses, *ib.*, *n*, *n*, leave by their interspace the floor of a neural canal, *n*, *c*, 1 inch 3 lines in extent, 15 mm. in breadth. The forepart of the sides of the centrum is smoothly concave, as if pinched in; the hinder half of the under surface shows the rough fracture whence a hæmapophysial element of some kind has been broken away.

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[*] 'Palæontology,' 8vo, 1850, p. 257

The hæmal arches preserved in succeeding caudal vertebræ are confluent with their centrum The dimensions of the biconvex fossil (Plate 35, fig 4) indicate a derivation from the smaller individual *Meiolania*. Its dimensions are:—

	Inch	Lines
Diameter of each terminal ball .	1	0
Length of the neural canal	1	3
Breadth of „ „	0	6

Three vertebræ, of probably the same individual as that which yielded the dorsal one, show, with characters relegating them to the caudal series, others, leading to the conclusion that the articular concavity of the centrum is at its hinder end, the convexity at its forepart; such conclusion is based upon the aspects of the articular surfaces of the zygapophyses and the direction or inclination of the neural and hæmal spines

The vertebra, Plate 35, figs. 5 and 6, here described, in size, texture, and correspondence of degree of concavity and convexity of the joint-ends of the centrum, I believe to belong to the same skeleton or species as those above described. The caudal character of the subject of figs. 5 and 6 is based on the presence of the hæmal arch, *h*, here confluent with the under part of that half of the centrum which is terminally excavated, fig. 6 *c′*, to receive the ball of the next vertebra. From the middle and upper part of the side of the centrum projects a transverse process, *d*, flattened vertically and terminating obtusely, this process is 1 inch in length, 7 lines in breadth. The piers of the hæmal arch, fig. 5, *h*, are continued without trace of suture from the hinder half of the under part of the sides of the centrum, and, sloping downward and backward, are confluent with a hæmal sub-compressed spine, *hs*; this extends in the same direction for 1½ inch below the concavity of the centrum, fig. 6, *c′*, and terminates obtusely with a slight expansion. The anterior opening of the hæmal arch is slit-shaped, 1½ inch in length, 3 lines in breadth, contracting to a point above and below; the posterior outlet, fig. 6, *o*, is an elongate triangle in shape, 6 lines across above, and pointed below.

The neurapophyses, *n*, *n′*, as in the dorsal vertebra, are confluent with the centrum, *c*; their bases extend along its anterior three-fourths and terminate in the ball, *c*; their antero-posterior extent is 1½ inch; from the fore part projects the prezygapophysis, *z*, with an elongate flattened articular surface looking upward and inward. A low oblique obtuse ridge extends along the neurapophysis from the prezygapophysis obliquely backward and upward to the base of the postzygapophysis, *z*, which has its flat articular surface turned outward and slightly downward.

A low antero-posteriorly broad neural spine, *ns*, rises from the hinder two-thirds of the neural arch, with an anterior trenchant border sloping to a thicker obtuse truncate summit; from the angles of the broader hind end of this spine two ridges, fig 6, *ns*, descend, each to the upper and back part of the corresponding postzygapophysis, *z*.

The size of the vertebra above described, from the summit of the neural spine, *ns*, to the end of the hæmal spine, *ns*, is 4½ inches, the length of the centrum is 2 inches 10 lines; the diameter of the terminal cup is 1 inch 5 lines; it is deep, hemispheroid, with a sharp well-defined margin; the opposite ball shows a corresponding size and convexity.

As this caudal vertebra shows no sign of confluence with an enveloping dermal bony ring, but every arrangement for motion upon coarticulated vertebræ, it may be inferred to have come from a fore part of a tail, where the dermal osseous girdles were free from the vertebræ they surrounded as well as from each other.

Another caudal vertebra with the same characters as in the preceding is indicated, by the smaller size of the transverse processes and the greater size of the hæmal arch and spine, to have been a succeeding one. More fragmentary specimens indicate a tail of the proportionate length of that in the *Crocodilia*

Limb-bones—The best preserved of the fossils indicative of bones of the limbs of *Meiolania* is an oblong one, Plate 36, fig 1, with well characterised proximal and distal ends, the former, fig 1, being the largest. This is terminated by a feebly undulate articular surface, fig. 1, *a*, 2 inches by 1¼ inch in its diameters. A rough insertional surface, fig. 2, *b*, projects for 3 or 4 mm from an extent of 1 inch 4 lines of the anterior border of the joint A second similar but shorter oblong surface, fig. 1, *c*, projects below the insertional margin of the proximal end. Besides the two oblong insertional tracts bordering the proximal articular surface, there is a third, fig 2, *d*, which extends from the narrower end of that surface 1 inch 9 lines down the corresponding border of the shaft; this is sub-compressed from before backward, convex across posteriorly; approaching to flatness across the proximal part of the opposite side. The shaft narrows to an obtuse margin at one side, is rounded across and thicker at the opposite side, of which the lower third develops a strong rough oblong sessile process, *e*, 1 inch in extent. The distal articular surface, fig 4, is undulate, 1½ inch by 10 lines in its diameters The only trace of fracture in this bone is at *d*, fig. 2, the upper end of the insertional surface extending down the narrower border of the shaft.

I have next to notice a limb-bone, fig. 5, 4 inches 3 lines in length, 10 lines across the narrowest part of the shaft, which expands to form a distal joint, 2 inches in breadth. A part of the thicker proximal end of the bone has been broken off; the slightly concave articular surface which remains measures 1½ by 1 inch. The above proportions bespeak a limb-bone about the same length as the preceding. What seems to be the distal end of this bone is obliquely truncate to form the joint surface, which is 1 inch 9 lines in length, 10 lines in breadth; a circular portion at one end of the surface is feebly concave; a similar portion at the opposite end is moderately convex; the intervening broader part is convex across the shorter diameters, concave in the opposite direction A non-articular part, *g*, extends partially beyond one end of the oblong articular surface, the opposite end forms a well-marked tuberosity. The indications of muscular attachments are those of forcible applications of the limb to which this bone belonged.

Dermo-skeleton.—A portion of the foremost, or one of the foremost, segments of the tail-sheath has been left free between the sacral dermo-skeleton and the anterior of the series of dermo-caudal segments. The terminal part of the osseous tail-sheath (Plate 36, figs. 1, 2, and 3), estimated by the pairs of processes, includes five anchylosed segments. The upper or dorsal tuberosities (*a* and *b*) are developed on three of these segments, the right tubercle projects from the fourth segment, the left being indicated by a low ridge and the groove dividing it from its fellow. On the fifth of this welded series the tuberosities are indicated by obtuse ridges and their dividing grooves, beyond which the sheath, which had gradually lost breadth and thickness, narrows to an obtuse end. In the first and second of these segments the lateral, *b*, as well as dorsal, *a*, tubers continue to be developed; in the third they are represented by ridges; in the fourth they are continued as low ridges to the end of the sheath. The contrast with the huge tuberosities at the corresponding part of the tail-sheath of *Megalania* is extreme.

The fore end of the foremost of the five segments, Plate 36, fig. 3, shows a thin obtuse margin, suggestive of some free motion of the so-armoured end of the Meiolanian tail. The free articular fore end of this terminal part of the tail-sheath shows the smooth inner surface, rather less curved, crosswise above; the wall of the cylinder gains thickness as it approaches the next segment, with which its anchylosis is complete, as is the case with the following four. The diameter of the fore end of the first segment is 3 inches 4 lines; the superiority of size over the corresponding vertebra of the endoskeleton is extreme. The neural spine of this vertebra, with apparently part of that of the succeeding one anchylosed therewith, has contracted confluence with the exoskeletal sheath, an attachment which extends across the portion of sheath contributed by the foremost and the next of the dermosteal cylinders.

The fore part of the thus imprisoned caudal vertebræ has been broken away, exposing a neural canal of 3 lines in transverse—its chief—diameter; the loose cancellous texture of the middle of the body of the vertebra partially fractured leaves an irregular cavity. The vertical diameter of the so-exposed part of the caudal vertebra is 1½ inch, the transverse 1 inch; there are short lamelliform transverse processes. The disappearance of whatever soluble tissues may have occupied the space between the endo- and exoskeletons of this portion of the tail leaves a cylindrical hollow with a smooth wall of the diameters above noted, to which the enclosed vertebra is partially attached; such cavity gradually contracts as it extends onward.

The upper surface of the tail-sheath, fig. 1, Plate 37, is longitudinally grooved. The sheath terminates in an obtuse cup of bone.

The chief desiderata for completion of Meiolanian osteology are the vertebræ of the trunk, the sternum, and the bones of the limbs; more caudal vertebræ are wanting to give the precise length of the tail.

The non-Chelonian pelvic characters and confluence, as in warm-blooded Vertebrates, of the constituent bones of the pelvis, are shown in Plate 32 of the 'Philosophical Transactions' for 1886. So far as the caudal parts of the skeleton are now known, both structure and proportionate length are Saurian, not Chelonian, the great development of the dermosteal part of the tail is Mega- and Meiolanian. Not an indication of those extreme modifications of combined endo- and exoskeletons, constituting the frame of the defensive chamber of the timid Tortoise, has yet come to hand. The best preserved trunk-vertebræ support each their pair of freely jointed ribs by distinct par- and diapophyses, as in the Crocodiles, Alligators, and extinct Dinosaurian Reptiles

I regard the modifications of trunk-vertebræ forming the basis of a "carapace" and a "plastron" as of more value in the ordinal distinction of the *Chelonia*, than the edentulous modification of the jaws But I fully recognise such cranial modifications in Megalanian and Meiolanian Reptiles as signs of a closer affinity to the *Chelonia* than have hitherto been detected in air-breathing cold-blooded Vertebrates.

The characters which have been detailed and illustrated in previous volumes of the 'Philosophical Transactions' may be, perhaps, deemed to support a distinct Reptilian sub-order, for which I venture to propose the name CERATOSAURIA; the representative genera at present recognised are *Megalania* and *Meiolania.*

ADDENDUM.

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The base of the skull gives characteristic evidence of the position of the extinct species in the Reptilian class. The position of the palatal nostril in the Chelonian order resembles that in the Lacertian; the narial passage descends from the outer nostril, is vertical, or nearly so, and opens upon the fore part of the bony palate; the maxillary as well as the palatine, with in some species also the premaxillaries as well as the vomer, contributing to form the palatal nostril.

In *Meiolania* the palatal nostril yields a Saurian character. From the single anterior nostril, which opens upon the fore end of the skull, the nasal passage is continued backward for 4 inches, and terminates in a transverse slit-like aperture, Plate 32; *h'*, $1\frac{1}{2}$ inch in extent, and one-third of an inch in vertical diameter. It is formed or bounded in great proportion by the pterygoids, and completed beneath by the palatines. The pterygoids extend about 1 inch further back, and terminate obtusely. The basis cranii between and behind these narrows from the basisphenoidal portion to the basioccipital, which terminates in the lower part of the condyle here visible.

The lower surface of those massive extensions of bone from the exoccipital and alisphenoid elements expand, as they recede from the cranium proper, to support the strong bony roof of the skull, from which the horny, defensive weapons are developed; these extensions contribute at their under surface the articular cavities for the condyles of the lower jaw

No cranium of a Vertebrate, which has come under my ken, has contributed so large a proportion of bone for mechanical needs outside, and in super-addition to, the parts forming the walls of the brain chamber.

The palatal or posterior opening of the nasal passages is anteriorly situated in *Chelonia* and *Lacertilia*, where those passages are vertical or nearly so, it is at the hindmost part of the bony palate in existing species of *Crocodilus*, and in a more advanced position, though still in the hinder half of the palate in the Mesozoic Crocodiles. In *Chelonia*, as in *Varanus* and most *Lacertilia*, its boundary includes parts of the vomer, the palatine, and maxillary bones, in *Iguana* it includes also part of the premaxillary. In *Crocodilus* it is wholly surrounded by the pterygoids; but in *Teleosaurus* the palatines combine with the pterygoids to complete it anteriorly.*

Description of Plates 31–37.

PLATE 31.

Skull of *Meiolania platyceps*, side view.

PLATE 32.

Skull of *Meiolania platyceps*, base view

PLATE 33.

Upper view of cranium, *Meiolania platyceps*.

PLATE 34.

Skull of *Meiolania platyceps*, back view.

PLATE 35.

Vertebræ of *Meiolania platyceps*.

Fig. 1. Front view of a dorsal vertebra.
Fig. 2. Side view of the same.
Fig. 3. Back view of the same.
Fig. 4. Centrum or body of the foremost caudal vertebra
Fig. 5. Side view of an anterior caudal vertebra.
Fig. 6. Upper view of the same vertebra.

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* "Fossil Reptilia of the Wealden Formations" (1873), p. 4.

PLATE 36.

Fig. 1 Proximal articular end of a limb-bone (*tibia*).
Fig 2 Front view of the same bone.
Fig. 3 Side view of the same bone.
Fig. 4. Distal articular end of the same bone.
Fig 5. Front view of the radius
Fig 6 Distal articular end of the same bone.
Fig. 7. Sternal arch, front view.
Fig. 8. Left end of the same bone
Fig. 9 Right end of the same bone.
Fig. 10. Dermal ossicle of trunk

PLATE 37.

Coalesced terminal segments of the dermal bony tail-sheath.

Fig. 1. Upper view.
Fig. 2. Side view.
Fig. 3. Anterior end view, with coalesced endoskeletal vertebra.

(All the Figures are of the natural size)

VIII. *On the Sexual Cells and the Early Stages in the Development of* Millepora plicata

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Communicated by Professor M FOSTER, *Sec. R S*

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[PLATES 38, 39]

UPON the edge of the fringing coral reefs which run along the southern shore of Talisse Island (N. Celebes), I found considerable quantities of a large handsome *Millepora* growing vigorously. The form seems to correspond very closely with the *M plicata* of MILNE EDWARDS (8)*, the most striking feature of which is that it is "plissé près des bords et donnant naissance à quelques lobes verticaux qui se détachent à angle droit de chaque surface des feuilles en forme de crêtes"

I broke off several pieces of these and preserved them either in absolute alcohol alone or in alcohol after treatment with corrosive sublimate.

I never saw the zooids properly expanded, either when they were living in their natural position on the reefs or in my aquaria.

Upon making a rough examination, by means of the very imperfect methods at my command in my little hut in the tropics, I found that the species is hermaphrodite, both ova and spermoblasts being present in the cœnosarcal canals This result was sent as a short note to the Royal Society in December, 1885 (10).

Our knowledge of the soft parts of the genus *Millepora* is due to the investigations of L. AGASSIZ (1) and to the excellent Memoir of MOSELEY (13), but neither of these authors, nor NELSON and DUNCAN (14) were fortunate enough to discover the sexual organs.

On my return from the tropics I commenced a series of observations in the University Museum at Oxford, and continued them in the Morphological Laboratory at Cambridge, upon the origin of the sexual cells in this species and the early stages of its development. Unfortunately, my work was much delayed by finding that several of the specimens were sterile, so that I have been occupied nearly twelve months in making my series complete, in establishing my results, and confirming my conclusions. It is my intention at some future date to publish an account of my observations upon the general anatomy of the hard and soft parts of this species of *Millepora*. In this communication I intend to confine myself to a consideration of the male and female sexual cells and their maturation, the impregnation of the ovum, and the early stages in the development.

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* The numbers in parentheses refer to the Literature List at end of paper.

The Sexual Cells.—Both male and female sexual cells arise in the *ectoderm* of the cœnosarcal canals, which anastomose between the dactylozooids and the gastrozooids. They commence as undifferentiated small cells (Plate 38, fig. 3, *s.c.*) lying on the mesoglœa between or beneath the ectoderm cells, and may readily be distinguished by their homogeneous structure and the readiness with which they stain in Borax carmine. The young ova, distinguished from the young spermospores by their small clear nucleus, become spindle-shaped at an earlier period, and may be seen to penetrate the mesoglœa to take up a position in the endoderm (fig. 3 *s c*^{1}.).

The young male sexual cells or spermospores generally attain to a greater size than the young ova before they penetrate the mesoglœa, and are distinguished by their large nuclei containing a coarse protoplasmic meshwork (fig. 6 *sp.*).

As soon as the young spermospore has taken up its position in the endoderm the nucleus increases considerably in size (fig. 7 *sp.*). The protoplasmic meshwork next splits up into a number of hook or rod-shaped pieces (fig. 8), and these divide again into a large number of very small particles (fig. 9). At this period these small nuclei fragments occupy the whole spermospore, which is surrounded by a thin structureless membrane.

The spermospores now migrate, probably in an amœboid manner, along the canals to the zooids. In most cases they choose the dactylozooids, but in one or two instances I have found them in the gastrozooids. At first they are to be found in the basal endoderm (fig. 1 *sp.*), but subsequently they pass into the cavity of the zooid. At about this period the surrounding membrane of the spermospore disappears, and a swarm of young spermoblast occupy the cavity of the zooid. The outlines of these are difficult to see when they are *en masse*, but their structure can be well seen where a few are scattered about at the edge of a torn section. Again entering the endoderm, they push out the mesoglœa into a number of diverticula between the tentacles, in which they remain until they are mature. These diverticula or sporosacs (fig. 12) vary considerably in number. Sometimes there are as many as four or five, but more usually only one or two. I have been unable to find any trace of the formation of a sporosac before the advent of the spermoblasts. It seems as if the spermoblasts were the active agents in the formation of the sporosacs, that, in other words, the spermoblasts do not migrate to any locality or structure already prepared for them, but choose for themselves a locality or localities which can readily be pushed out into the form of sporosacs. It is difficult to say very definitely whether the spermoblasts themselves actually perforate the mesoglœa to take up a position in the ectoderm, but I believe they do not. The wall of the sporosac seems to me to be always continuous with the mesoglœa of the body wall. There is nothing present in the sporosac at all comparable with a spadix, nor is there any other evidence of the sporosac being a degenerate medusiform gonophore.

The Ova—The young ova, having penetrated the mesoglœa of the canals in the germinal region, increase in size rapidly (figs 3 and 4). As they increase in size they become stalked, the stalk remaining attached to the mesoglœa. This stalk of the ovum is not a separate structure but simply a pseudopodium modified for the purpose of retaining the ovum in position. It might be compared with the stalk of an Infusorian. A structure probably similar to this has already been described in the ova of *Myriothela* by ALLMAN (3)

I am not certain at what period, but certainly some time before maturation, the ovum changes its position in the canal by amœboid movement (fig. 5) The ovum throws out pseudopodia, withdraws its stalk, and wanders away to a more favourable locality, where it again settles down as an oval stalked ovum

Maturation takes place while the ovum is at rest.

The germinal vesicle, which in immature ova is very distinct, becomes obscured (Plate 39, fig. 14, D) and eventually disappears (fig. 14, E). A spindle-shaped structure with longitudinal striæ next appears in the middle of the ovum (fig. 14, F), and this gives off the first polar globule. In the next stage the spindle-shaped structure is much longer but more indistinct (fig. 14, G), this gives off the second polar globule, and the spindle is dispersed. During the formation of the second spindle, and subsequently, the substance of the ovum becomes clouded and heterogeneous, as if some considerable disturbance of the protoplasm was going on.

After the dispersion of the second spindle, impregnation takes places It is very probable that at this stage the ovum withdraws its stalk again, and wanders in the lumina of the canals in search of the spermatozoa, for I have never found one with a stalk. The heads of the spermatozoa enter the ovum, leaving their tails on the surface When the head of the spermatozoon is within the ovum it appears as a dark corpuscle which stains deeply, surrounded by a clear transparent space. As many as three or four spermatozoa may thus enter the ovum, but whether they all take part in impregnation, or are all but one of them discharged again, I cannot tell (fig. 14, J and K)

After impregnation the ovum again becomes clear and homogeneous, and the nucleus reappears (fig. 14, L). It would be difficult to distinguish an ovum at this stage from an ovum just before maturation, were it not for the presence of remains of the polar globule. The nucleus, soon after its reappearance, is seen to be filled with a number of small spherical bodies like nucleoli (fig. 14, M). The wall of the nucleus next disappears, and these spherical bodies, together with a number of very small fragments, are seen scattered about in the region of the ovum formerly occupied by the nucleus (fig. 14, N). Later, they migrate towards the centre of the ovum, where they form an equatorial zone of two or three rows (fig 14, O, P and Q). This zone divides into two clusters of fragments which, travelling first to the two poles (fig 14, R), eventually are scattered over the whole ovum (fig 14, S).

At this stage, but not before, it is possible to discern in favourably stained specimens certain faint shadings in the substance of the young embryo, which indicate that each fragment is surrounded by its own proper protoplasm. The fragments have grown to such a size as to enable us to call them nuclei, and the young embryo has reached a stage which corresponds with the morula stage of other embryos.

At this period in the development the stalk is withdrawn, and the embryo generally wanders into the neighbouring gastrozooid, where it either fixes itself again to the basal mesoglœa or lies unattached in the basal endoderm (fig 2) The nuclei next arrange themselves circumferentially so as to form a solid blastosphere

At this period I believe most of the embryos are set free, probably as ciliated larvæ, being discharged into the sea by the mouth of the gastrozooid.

Were they discharged as the spermatozoa are from a sporosac on the body wall, I must have found at least one example in many hundred preparations; but not only have I found no female sporosacs, but also not one single embryo in a gastrozooid in any other position than in the basal endoderm.

Sometimes the embryos seem to remain a long time in their position in the basal endoderm of the gastrozooid. In one example I found three or four embryos nearly twice as large as the mature ovum. In one of them there was a slight invagination of the nuclei at one point, accompanied by a proliferation of the nuclei there (fig 14, W). Later stages in the development are unknown to me.

The Origin of the Sexual Cells.—My investigations upon the sexual cells support the views of the Hertwigs (9) and Weismann (15), that the sexual cells of the Hydromedusæ originate consistently in the ectoderm. I am inclined to agree with the suggestion of Weismann (15) that in the ancestral forms of the Hydromedusæ all the sexual cells originated in the ectoderm, and were ripened in and eventually discharged from that tissue, without entering into any other.

The reason for the wandering of the sexual cells in *Millepora* from the ectoderm to the endoderm must be sought for in the presence of a hard, inflexible, calcareous exoskeleton.

The corallum or cœnenchym (Moseley) of the *Millepora* is undoubtedly a product of the ectoderm of the cœnosarcal canals, and it seems most probable that the proper growth and nutrition of the young sexual cells would be seriously interfered with by contact with such a substance, were they to remain in the ectoderm.

Consequently we find that at an early stage they perforate the mesoglœa to take up a position in the endoderm. Whether this is a sufficient and the only cause of the migration of the sexual cells it is impossible to say.

I am inclined to believe that the possibility of better nourishment in the endoderm should be taken into consideration. Professor Weismann (15) maintains that in the Tubularian Hydroids there is no difference in the nourishing powers of the ectoderm and the endoderm. It is true, as he points out, that these cells do not feed in an amœboid fashion upon unprepared food, but are only nourished by the fluid or chyme prepared by the action of the endoderm cells.

But surely there must be more of this fluid in the tissue which prepares it than in the tissues to which it is distributed There must be more surplus chyme in the endoderm, which has to supply the whole organism, than in the ectoderm, which has to seize and appropriate only what is brought to it

That the rapid absorption of a large amount of nutritive material is of the utmost importance we see from many examples, but none more striking than that of *Hydra*, which, according to KLEINENBERG (11), throws out a considerable number of pseudopodia to increase its absorbing surface

Perhaps it is premature, however, to say definitely that the endoderm does afford more nourishment for the sexual cells than the ectoderm; but as it seems to me to be quite possible, if not highly probable, that it does, we cannot dismiss this as an impossible cause of the migration of the sexual cells until we have some definite grounds for saying it is not.

The Ova.—The pseudopodia and the peculiar stalk of the ova of *Millepora* are not altogether unknown in other types. Thus, the ova of *Hydra* (11) and *Halisarca* (17) possess pseudopodia, and, according to WEISMANN, the ova of some Tubularian Hydroids wander in the colony in an amœboid manner.

The stalk of the ovum of *Millepora*, to which a similar structure exists in *Myriothela* (3), simply serves to keep the ovum in its proper position in the canal. It seems to be sometimes completely withdrawn when the ovum migrates, and to be re-formed when the ovum comes to rest. It is, in fact, simply a pseudopodium modified to keep the ovum in its position in the endoderm.

The Maturation and Impregnation of the Ovum do not offer any striking peculiarities. The formation of the nuclear spindles was difficult to observe, as my specimens were not specially prepared for this kind of minute histological investigation; but from what I was able to observe in well-stained specimens, with a high power, I should think that the history of the formation of the nuclear spindles does not differ materially from what has been described by other authors in other ova.

That the two polar globules are not always seen at the same point is not peculiar to *Millepora* (*cf.* CARNOY (6), vol. 2).

The absence of any true segmentation in the ovum of *Millepora* is a very striking phenomenon, because it is not associated with the presence of a considerable amount of yolk.

The ova are only ·01 mm. in diameter, and contain none of the yolk spherules or granules which are so commonly present in the ova of other Hydroids.

The ova of some other Hydroids are known to develop without segmenting. Thus, in *Myriothela*, KOROTNEFF (12) says, "Nach der Befruchtung kommen in dem Entoplasma Zellen vor (wahrscheinlich nach der Art der freien Zellenbildung) die sich theilen und deren Abkommlinge sich gegen die Peripherie des Eies bewegen und in das feinkornige Ectoplasma ubergehen und da ein Blastoderm rund um das Ei bilden."

In this case, however, the egg contains a considerable amount of yolk, and the formation of the blastoderm is probably comparable to that of certain Crustacea (*Eupagurus Prideauxii*) and Insects (*Tetranychus telarius*) (4).

The peculiarity of the ovum of *Millepora* is that it is a small egg with little or no yolk, in which complete division of the nucleus into numerous nuclei takes place, without any apparent division of the ovum itself.

In this respect it is unique, and the question arises whether we must believe that the ovum of the Millepore is an ovum which formerly possessed a large quantity of yolk and has subsequently lost it, or whether the segmentation of the ovum has been lost from other causes

In the first place, it does not seem to me to be a necessary conclusion that, because the ovum exhibits phenomena which can be paralleled only by telolecithal or centrolecithal ova, that therefore the ovum must have contained in bygone times a considerable amount of yolk

In the second place, the loss of segmentation may have been caused by the migration of the egg after the early stages of development have commenced.

And thirdly, the evidence before us indicates that the Millepore ovum never passed through a stage with much yolk.

These three points must be considered a little more in detail. The complete segmentation of an ovum must be considered to be rather of the nature of a repetition of phyletic history, than a necessary process in the formation of an embryo.

It is impossible to imagine *à priori* any definite use which the complete segmentation of the ovum can be in the building up of animal tissues.

Every ovum upon fertilisation, or even before, must possess a tendency to pass through all the stages in the phyletic history of the animal. If it did not possess this tendency, we should have lost all traces of an animal's history in its ontogeny There would be no gill slits in Mammalian embryos, no pineal gland in Vertebrates. The science of Embryology would be of little value to us.

We know that this tendency may be overcome, by the fact that many stages in ancestral history, many organs and structures undoubtedly possessed by ancestors, disappear. But what causes govern the obscuration or disappearance of these organs, structures, and stages, we do not, in most cases, know with any degree of certainty.

Turning now to the stages represented in the various phases of segmentation and the morula.

Most ova with but little yolk completely segment; the tendency to repeat ancestral types is not interfered with. Most ova with a large amount of food-yolk do not segment; the tendency to repeat ancestral types is interfered with. The natural conclusion to come to is, that in such cases this tendency to repeat ancestral types is interfered with by the food-yolk; that the delay, which would be occasioned by the complete separation of considerable amounts of yolk, is of such disadvantage to the animal that the tendency to repeat ancestral types is overcome and lost. But this is not necessarily the only cause which can bring about this result.

It is very probable that limited space, or a migration of the young embryo, would bring about the same result; because, in the first place, an unsegmented ovum would occupy less space than a segmented one, and in the second place, an unsegmented ovum would move with much greater facility and less friction.

Now most ova do not move immediately after they are fertilised, and consequently they usually occupy a place either within or without the body of the mother, which is of sufficient size for the accommodation of the embryo when it is older and larger, consequently, in nearly every case, the ovum segments when it is not charged with yolk.

Even the ovum of Mammals, which we have good reason to believe formerly contained much yolk, segments. The tendency of the ovum to repeat ancestral types being no longer checked by the yolk nor by any other cause.

In *Millepora* we have an example of an ovum which is not only matured and fertilised in a confined space—the cœnosarcal canals—lined by solid carbonate of lime, but also has to migrate to the gastrozooids after the early stages of development have commenced.

These facts are, I think, quite sufficient to account for the absence of segmentation.

But what evidence have we that the ovum of *Millepora* never did contain a large amount of food yolk ?

In the first place, had the ovum of *Millepora* ever been much larger than it is at present, it must have possessed either ampullæ or larger canals. Not a trace of these is to be found in *M. plicata*, the only species of which the sexual cells have been examined.*

Had these ever been developed it is most probable they would have been retained, and the ovum, having more space for its development in the early stages, would have segmented, as the ovum does in Mammalia.

But it is difficult to frame any reason to explain why the ovum of a Hydroid having once acquired yolk should lose it again, such as we can put forward in the case of the Mammalian ovum.

Lastly, I believe that the general anatomy of *Millepora* indicates that this Hydroid is of a very old type, and has come down to us from pre-eocene times almost unchanged.

The curious phenomena which have been described, in connection with the fragmentation of the germinal vesicle after impregnation, are so important and so strange that I dare not offer any explanation of them before trying other methods of treatment

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* It is possible that the ampullæ described by QUELCH (16) in *M. Murrayi* may have been produced by parasitic growth, or that, if they are true ampullæ, the species may be a more modified one than *M. plicata*, and possess ova with food-yolk, but this cannot be determined until the soft parts of *M. Murrayi* have been examined

It is possible that the processes of nuclear division are accelerated by the absence of yolk and segmentation.

The Development of the Spermatozoa —The view that the ovum does not segment on account of its migrations is supported by the history of the development of the spermatozoa.

In most animals the division of the nucleus of the spermospore is accompanied by its segmentation into a sperm morula or spermosphere (*cf.* BLOMFIELD (5) and GILSON (6)).

In *Millepora* the division of the spermospore into a sperm morula does not take place, the spermoblasts being formed by the rupture of the spermosphere at a very late period. It is highly probable that this is due to the same cause as the similar phenomena in the development of the ovum, and this cause is the wandering or migration that takes place through narrow channels before they reach their ultimate position in the zooids.

The Zoological position of Millepora.—The very prevalent idea that *Millepora* and *Hydractinia* are related to one another, must now be abandoned. The skeleton formed by the former is calcareous, by the latter chitinous, the zooids of *Millepora* are very different in character from the zooids of *Hydractinia*, and lastly the phenomena of sexual reproduction in the two genera are totally different. Indeed, beyond the facts that they are both Hydrozoa with dimorphic zooids and a certain similarity of growth, there are no points of relationship between them.

I am inclined to believe that the Milleporidæ, together with the Stylasteridæ, belong to a separate stock altogether from the Hydromedusæ, a stock which never possessed *medusæ* or *medusiform gonophores.* To this point I purpose to return in a subsequent Memoir.

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13. Moseley, H. N. Report on certain Hydroid Alcyonarian and Zoantharian Corals. Zoology of H.M S. "Challenger," Part 7
14. Nelson, R. G., and Duncan, P. M. On the Actinozoan Nature of *Millepora alcicornis*. Ann. Mag Nat. Hist., vol. 17, 1876, p. 354.
15. Weismann, A. Die Enstehung der Sexualzellen bei den Hydromedusen Jena, 1883.
16. Quelch, J J. On the Presence of Ampullæ in *Millepora Murrayi*. Nature, vol. 30, p. 539
17. Schulze, F. E. Die Gattung Halisarca. Zeitschr. Wiss. Zool., vol. 28, 1877, p 1.

Explanation of Plates 38 and 39.

The following lettering is used throughout .—

A.	Albuminous sheath of the embryo in fig. 14, W.
emb.	Embryo in the basal endoderm of the gastrozooid
End.	Endoderm of the zooids.
Ect.	Ectoderm of the zooids.
end.	Endoderm of the canals.
ect.	Ectoderm of the canals.
fr.	Fragments of the nucleus.
gr.	Germinal vesicle.
M.	Mouth of the gastrozooid.
m.	Mesoglœa.
N.	Large nematocyst.
n.	Small nematocysts of the tentacles.
Nu.	Nuclei of the embryos.
ov.	Ova.
p.	Pedicle or stalk of the ovum.
p g.	Polar globule.
S.c.	Sexual cells lying in the ectoderm.
S.c.^{1}	Sexual cells perforating the mesoglœa.
sp.	Spermospore.
sp b.	Spermoblast.
spi.	Spindle.
spz.	Spermatozoon
S.s.	Sporosac.
t.	Tentacle.
z.	Zoanthancellæ.

PLATE 38.

Fig. 1 Longitudinal section through a partially retracted dactylozooid of *M. plicata*, showing a nearly mature spermospore in the basal endoderm. × 200 diam.

Fig 2. Longitudinal section through a partially retracted gastrozooid, showing two young embryos lying in the basal endoderm. × 200 diam.

Fig. 3. Longitudinal section through a portion of a cœnosarcal canal in the germinal region, showing the young sexual cells (*sc.sc*) lying in the ectoderm, and one (sc^1) penetrating the mesoglœa to take up a position in the endoderm.

Fig. 4. Two young ova lying in the endoderm of a canal and attached to the mesoglœa by a stalk (*p.*).

Fig. 5. An ovum changing its position in the canal by amœboid movements. In the last two figures the zoanthancellæ have been omitted.

Fig. 6. Section through a small portion of a canal wall, showing a young spermospore lying in the ectoderm.

Fig. 7. Section through a portion of a canal showing a young spermospore lying in the endoderm The nucleus is large and contains a coarse protoplasmic meshwork.

Fig. 8. Section through a portion of a canal, showing a young spermospore at a later stage than in fig. 7, the protoplasmic meshwork having split up into a number of loops or rods.

Fig. 9. A spermospore at a still later stage. The fragments of the nuclear meshwork are now much smaller, more numerous, and occupy nearly the whole spore.

Fig. 10. Transverse section through a canal, showing a nearly ripe spermospore wandering in the lumen. The fragments of the nucleus are now scattered throughout the whole of the spore, but a thin spore-wall keeps the contents together. × 200.

Fig. 11. Longitudinal section through an expanded dactylozooid with a swarm of young spermoblasts occupying its cavity. × 200.

Fig. 12. Longitudinal section through another expanded dactylozooid in which the young spermoblasts are situated in four sporosacs between the tentacles.

Fig. 13. *a.* Spermoblasts of *Millepora*, as they appear when the ripest sporosacs are broken artificially.

b. Spermatozoa of *Millepora* (?) found in the canals.

[I place (?) after *Millepora* because it is impossible for me to say for certain to what animal stray spermatozoa in the canals of a Millepore may belong, but it is highly probable that the ones figured are really the spermatozoa of *Millepora.*]

PLATE 39

Fig. 14 A series illustrating the maturation, impregnation, and early stages in the development of the ova of *Millepora*

A.B.C Three ova before maturation, all with a well-marked germinal vesicle. A. An ovum at rest and attached to the mesoglœa by a stalk. B. An ovum, also attached by its stalk, but which has thrown out pseudopodia. C An ovum wandering in the canal by means of its lobose pseudopodia.

D. An ovum in which the germinal vesicle is becoming matured previous to maturation.

E. An ovum in which the germinal vesicle has completely disappeared.

F. An ovum in which the first spindle has appeared, and a projection on the surface of the ovum just opposite one end of it, which marks the position of the discharge of the first polar globule, *p.g*^{1}.

G. An ovum, showing the second spindle stretching across the whole length of the ovum and just giving rise to the second polar globule, *p.g.*^{2}

H. An ovum, showing the dispersion of the spindle after the discharge of the second polar globule.

I An ovum, mature and ready for impregnation.

J.K. Two ova, into which the heads of the spermatozoa (*spz.*) have entered. The head of each spermatozoon appears as a dark corpuscle surrounded by a clear space.

During stages G–K the ovum, which was previously clear and homogeneous, becomes clouded and heterogeneous.

L. An ovum, showing the appearance of the nucleus after impregnation.

M, An ovum in which the nucleus contains a number of nucleolus-like bodies.

N. The fragmentation of the nucleus. The wall of the nucleus has disappeared, and the nucleolus-like bodies or fragments of the nucleus are scattered over the proximal end of the ovum.

O. The fragments are travelling towards the equatorial plane of the ovum.

P.Q. The stages in which the fragments are arranged in an equatorial zone.

R. The stage in which the fragments are situated in two polar zones.

S. The stage in which the fragments of the nucleus may be fairly called the nuclei of the embryo and the embryo a morula. Very faint shading between the nuclei indicates the limits of each cell

T.U. The nuclei in these stages approach the circumference of the embryo. No blastocœl can be distinguished

W. Latest stage in the development of the embryo observed. *Nu.* Circumferential nuclei. *Nu.*^{2} Nuclei lying in the central mass of the embryo. *Nu.*^{3} Nuclei invaginating and proliferating at one point.

A. Albuminous sheath surrounding the embryo *p.* remains of the stalk of the embryo.

IX. *A further Minute Analysis by Electric Stimulation of the so-called Motor Region of the Cortex Cerebri in the Monkey* (Macacus sinicus).*

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(From the Laboratory of the Brown Institution.)

Abstract received and read June 16,—Full paper received August 12, 1887

[PLATES 40–42.]

INTRODUCTION

IN a former paper published in the 'Philosophical Transactions,' B., vol. 178 (1887), pp. 153–167, a minute account was given by us of the effects produced by electrical stimulation of the so-called motor area in the cerebral cortex for the upper limb. In continuation of this work we have investigated in a similar manner the effects produced by stimulating the rest of the so-called motor region on the convexity of the cortex, with the exception of the lower parts of the ascending frontal and parietal convolutions The parts examined in the present research comprise the posterior third of the frontal convolutions, the upper third of the ascending frontal convolution, the superior parietal lobule, and the posterior half of the ascending parietal convolution. The movements evoked by stimulating these areas were respectively those of the head and eyes to the opposite side, conjoined movement of both opposite limbs, movements of the lower limb, and movements of the upper limb. In order to avoid discrepancies in the arrangement of the cerebral sulci in different species, and so to obtain exact localisation of the effect produced, the same variety of Monkey was alone used, viz., *Macacus sinicus.* In all we have performed twenty-three experiments, the animal in each case having been narcotised with ether and killed before recovery from the anæsthetic.

PART I.—ANATOMY

In the paper above referred to, a description was given of the position in the Monkey of the fissure of ROLANDO, the præcentral sulcus, and a small fissure above this, called by Professor SCHAFER "*x*." The excitable region investigated in the present paper is limited below, where it lies in front of the præcentral sulcus, by the horizontal level* of the lower end of that sulcus, the superior and anterior part being bounded above by the middle line, and in front by a sulcus which Professors HORSLEY and SCHAFER provisionally named "*y*" (see fig 1). Below, it is partially bounded by a sulcus which we have temporarily called "*w*." This sulcus, "*w*," runs horizontally from near the tip of the frontal lobe backwards to within a very short distance of the vertical limb of the præcentral sulcus, thus lying below and approximately parallel to the upper limb of the præcentral sulcus. The homology between this sulcus and corresponding parts of the human brain has not as yet been made out. The middle part of the region investigated in the present research is bounded above

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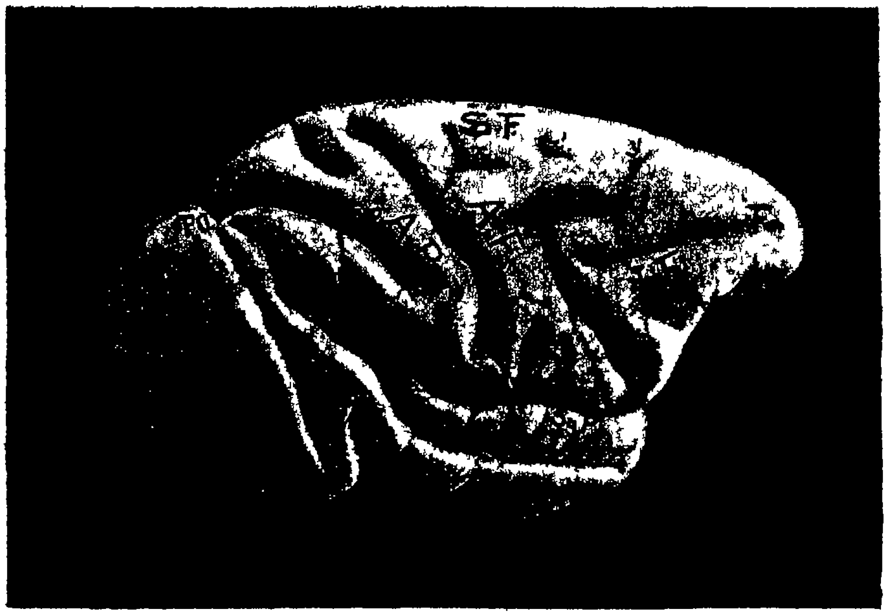
* The expenses of this research were defrayed by a grant from the British Medical Association.

Fig. 1



Photograph of the external surface of the right half of the brain of a Monkey (*Macacus sinicus*).

Sulci	SyA.	Fissure of SYLVIUS, anterior limb.	
	SyP.	Fissure of SYLVIUS, posterior limb	
	R.	Fissure of ROLANDO	
	PO.	Parieto-occipital fissure	
	IP	Intra-parietal sulcus	
	Pc	Præcentral sulcus	
	v.		Sulci, so named
	w		
	x.		
	x′	Supplementary to *x*, occasionally found	
	y.		
	z		

Convolutions or Gyri	F.	Tip of frontal lobe.	SF.	Superior frontal.
	IF.	Inferior frontal	AF.	Ascending frontal
	AP.	Ascending parietal.	O.	Occipital lobe

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* I.e., a line parallel to, and a short distance above, the Sylvian fissure

by the longitudinal fissure and below by the sulcus "x." The remaining part of this region, situated behind the fissure of ROLANDO, is bounded above by the longitudinal fissure, behind by the intraparietal sulcus, and below by the horizontal level of the lower end of that sulcus. The upper part of the ascending parietal convolution, or as it is also called the superior parietal lobule, is divided by a small sulcus which is usually vertical, and which has been designated "z" by Professors HORSLEY and SCHAFER (see fig. 1).

(As we showed in our previous paper, we consider that the sulcus "x" separates the superior from the middle frontal convolution, and is consequently homologous with the superior frontal sulcus of Man.)

On looking at fig. 1 it will be seen that the portion of the cortex treated of in this paper partly surrounds the area in which the upper limb is chiefly represented—as described in our former paper—on two sides, viz., in front and above. These parts of the cortex in front and behind the area for the upper limb form the anterior and posterior limits respectively of the cortex which is excitable. The present research completes the investigation of the upper part of the excitable region of the outer convex surface of the hemisphere.

TOPOGRAPHICAL DETERMINATION OF THE SULCI.

The position of the sulci in different Monkeys of the same species and of about the same age varies considerably. These variations were noted in the following way:—the brain of each Monkey was exposed, and the part to be investigated was drawn the exact size, the distance of the sulci from each other and the size of the convolutions being measured by compasses; thus an accurate representation of each individual brain was recorded. As can be well seen by referring to figs. 1A and 1B, noteworthy variations in the outlines of the sulci were thus revealed.

Fig 1A.

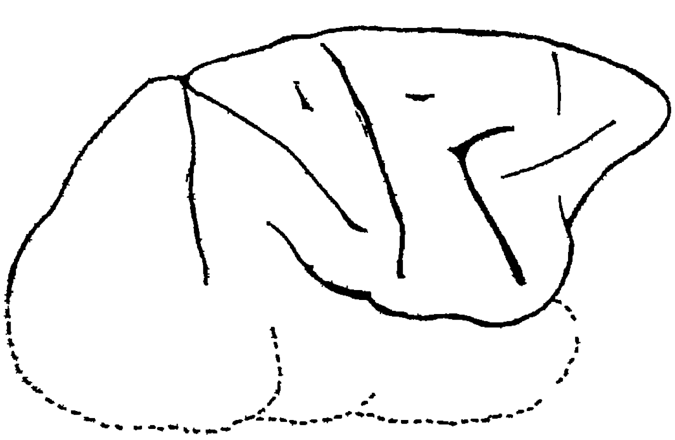
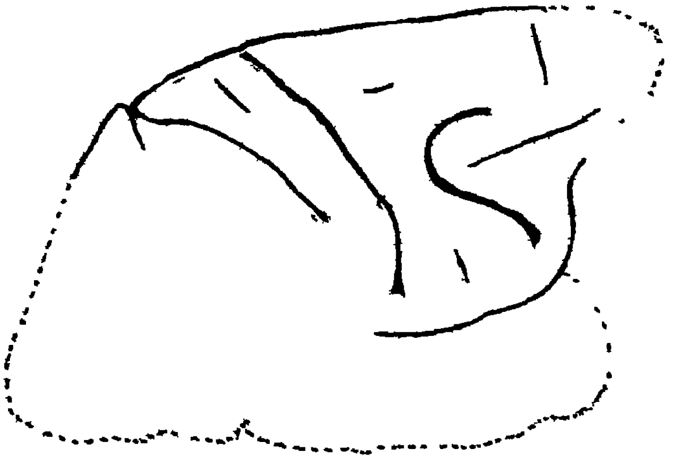


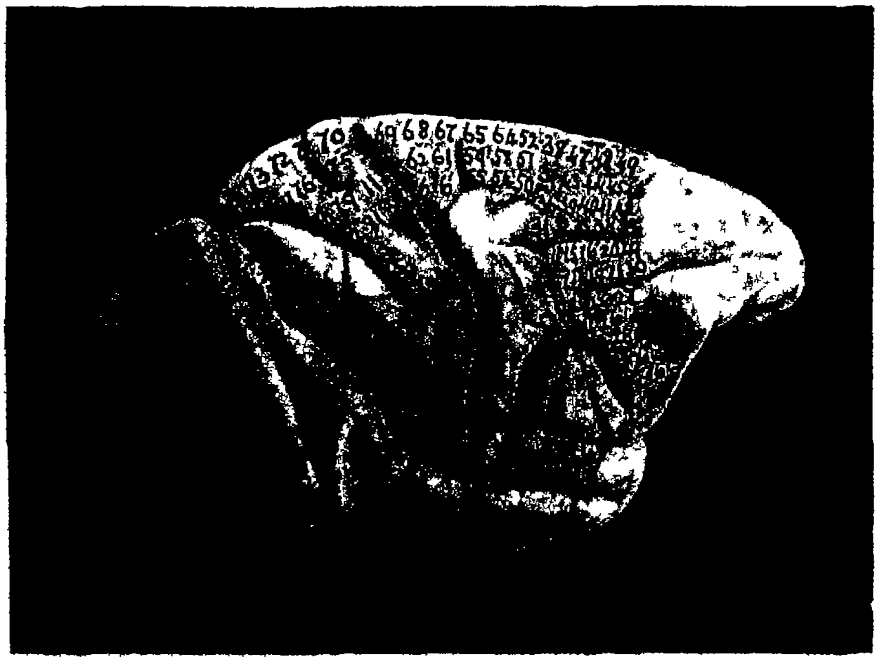
Fig 1B.



PART II—METHOD OF NOTATION OF THE VARIOUS POINTS STIMULATED

Method of Experimentation.—We have, as before, divided up the area to be examined into centres* of 2 mm. square, but, although in our former research we investigated the contiguous borders as well as the middle point of these minute divisions, we thought it sufficient then to record only the latter half of these observations. In describing our present research we have thought it better to record the result obtained at every point stimulated. Consequently, in any given linear centimetre there will be five points of stimulation. that is to say, the electrodes being as before, 2 mm. apart, the middle of each centre will be 2 mm. distant from the middle point of an immediately contiguous one. The mere difference in size of the brain of some of the Monkeys investigated compelled us to slightly alter this arbitrary arrangement by suppressing a row of these centres where the approximation of the sulci reduced the surface area of the excitable cortex, so that there was only room for two in place of three rows of numbers. Moreover, occasionally we have been compelled to spread out the numbers, but the error of position so caused was never more than ·5 mm. As the method of notation of these small centres was quite arbitrary, and as numbers had to

Fig 2.



This is a similar photograph to fig. 1, and shows the area of the cortex, which is the subject of this paper; the numbers denote the different individual points of stimulation, of which 74 are here given. Each number denotes a centre of the size of 2 sq mm. Centres 35, 42, and 46 apparently pass anterior to the sulcus *y* (see fig. 1), but the deep shadow is caused by a large vein which happened to be present in this brain.

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[*] By the word centre, we mean each of the 2 mm. square divisions into which we have partitioned the region investigated. We reserve the term area to designate the total cortical surface in which movements of one part (*e.g.*, a limb) are wholly represented, *i.e.*, the upper limb area, the face area, etc.

be occasionally omitted owing to the inequalities and irregularities of a convex surface such as that of the brain, it has been impossible to maintain a perfect continuity in sequence of the numbers employed. (Reference to figs 1 and 2.)

Method of Stimulation.—We have used as before the faradic current, employing such an one as would only just evoke a movement, and for the detection of the primary movement (see 'Phil Trans.,' *l c.*, p. 163) the method of momentary application of the stimulus. The sole change made in the apparatus has been the substitution of one litre bichromate of potash cell for the single DANIELL cell.

The parts of the cortex relegated to the representation of the various parts of the body observed to move on excitation of the different centres must now be described, in order to make clear the details of the subsequent analysis.

PART III.—THE TOPOGRAPHY OF THE REPRESENTATION OF THOSE PARTS OF THE BODY, OF WHICH MOVEMENTS WERE OBSERVED IN THE PRESENT RESEARCH.

(See fig 3)

(I.) *The Head and Eyes.*—The area of representation of the fundamentally important movement of turning the head and eyes to the opposite* side is a very extensive one, reaching from the longitudinal fissure above almost to the fissure of SYLVIUS below It is limited in front and above by the small transverse or perpendicular sulcus *y* before referred to. The limitation anteriorly is continued downwards, in the same direction as *y*, to the horizontal sulcus which we have called *w*, along which the imaginary boundary runs backwards to the narrow gyrus surrounding the hinder end of this sulcus, and which bounds in front the vertical limb of the præcentral sulcus. Below *w* the border line of the area extends downwards parallel to the vertical limb of the præcentral sulcus, this portion of the line frequently corresponding with a small oblique sulcus which seems to us to be the anterior limb of the fissure of SYLVIUS. Posteriorly the area is limited by the vertical limb of the præcentral sulcus, and by a line continuing the direction of this same upwards to the middle line, passing a little in front of the anterior extremity of the sulcus *x* The area of representation of this part has, therefore, roughly speaking, the outline of a flag, the staff of which forms the lower part (see fig. 3).

The synchronous conjugate deviation of the eyes to the opposite side is represented in the same region, but to a less extent than the movement of turning the head (*vide* page 212).

(II.) *The Lower Limb.*—The area of representation of the movements of the lower limb is limited in front by a line passing vertically through the anterior extremity of the sulcus *x*, and sometimes a little in front of this point; behind, it extends to the junction of the intra-parietal sulcus with the longitudinal fissure; upwards it extends to the median line, where it is continuous with the marginal convolution, below it is limited by the sulcus x, and by an imaginary line drawn backwards from this across the fissure of ROLANDO and through the middle of the sulcus z to the intraparietal sulcus. The shape of the area is in the form of a horizontal strip along the top of the hemisphere.

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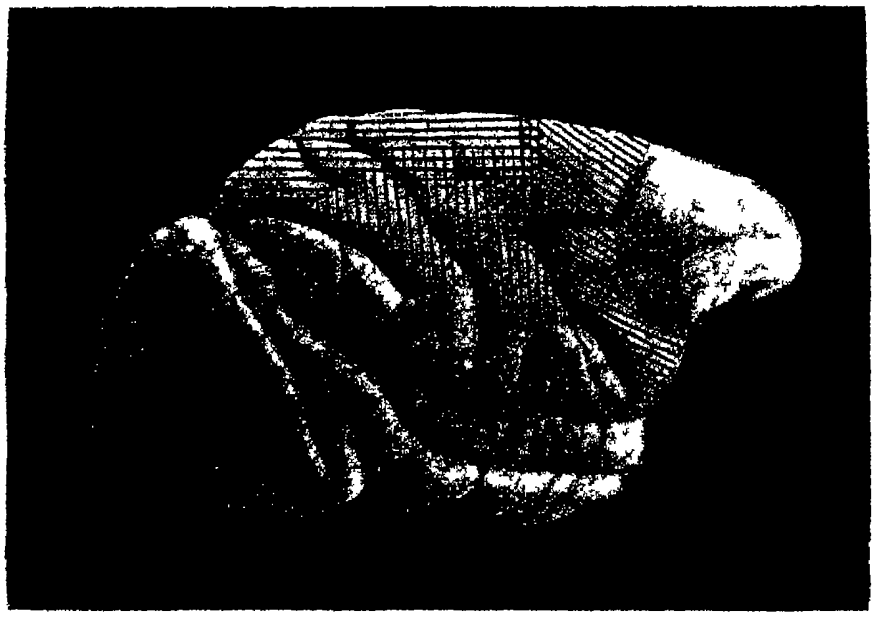
* By this is meant, of course, the turning away of the head so that the face looks away from the hemisphere stimulated

Fig 3



A similar photograph, shaded to show the parts of the cortex, excitation of which produces movements of the head and eyes to the opposite side, and movements of the upper and lower limbs, it comprises the areas which were investigated in our previous paper, as well as those which are the subject of the present one.

Oblique shading represents the area of the movements of the head and eyes
Vertical shading „ „ „ upper limb.
Horizontal shading „ „ „ lower limb

The places where the lines, having different directions, intersect, denote the overlapping of the contiguous areas; and at these points the functions of these different areas are represented together.

(III.) *The Upper Limb.*—The area of representation of this limb we have already described in part in our former paper, in which, however, we left for future observation the analysis of the margins of the upper limb region. This we have now done, and we find that the upper limb is represented over the whole of the ascending parietal convolution below the line given above in limitation of the representation of the lower limb. For the discussion of the limitation of the rest of the upper limb region see page 238, where the localities of the fusion of the different contiguous centres are treated of in detail.

We do not here treat of the area of representation of the face, jaws, &c., and the observations on these points will form the subject of a future paper.

PART IV.—REPRESENTATION OF THE MOVEMENTS OF THE HEAD ACCOMPANIED BY CONJUGATE DEVIATION OF THE EYES (Plate 40, figs 3, 4, 4A, 5.)

The movements of the head and eyes were observed by Professor FERRIER as being simultaneous. We find on further analysis that, though this synchronous action is by far of commonest occurrence, yet that considerable differentiation exists, and of this we shall now speak, reserving the discussion of the simultaneous movements to pp. 213 to 215, when we consider the march of movements in this region.

The different movements, therefore, which have to be considered in this part are—

I. *Movements of the Head.*—The head moves in one of the following modes or in combination of the same

(*a*) Simple horizontal rotation to the opposite side.
(*b*) Rotation with elevation of the muzzle.
(*c*) Rotation with adduction of head to the (opposite) shoulder.

II. *Movements of the Eyes.*—

(*a*) Both eyes open
(*b*) Both eyes turn horizontally to opposite side.
(*c*) Both eyes turn to opposite side and upwards.
(*d*) Both eyes turn to opposite side and downwards.
(*e*) Both eyes return to the middle line (from the side stimulated) or turn only through a few degrees.

III. *Movements of the Pupils.*—

(*a*) Contraction.
(*b*) Dilatation.

I. *Movements of the Head:*

(*a*) Simple horizontal rotation to the opposite side. This occurs as a primary movement most markedly in the part of the cortex above the horizontal fissure of the præcentral sulcus, *i.e.*, the middle frontal convolution, and especially in the centres 32, and to a slightly less degree in 33, 40, 44, and 45 (see fig. 2). This movement of turning the head to the opposite side is also represented* over the whole area included by the centres 14–52.† From this it follows that the principal focus of the representation of this act, as a primary movement, is most marked at centre 32, from which point the representation gradually diminishes (*vide* fig. 4).

(*b*) Rotation to opposite side with elevation of the muzzle. It is a matter of common observation that the movement of the head to either side is often accompanied by a tilting of the head backward so that the face looks upwards as well as outwards. We have never observed this elevation of the muzzle below the horizontal limb of the præcentral sulcus. Further, this combined action, we find, is most represented in the superior frontal convolution close to the margin of the hemisphere, and most especially in the centre 48, in addition it is present in the centres 38, 47, 44, 45, 40, 41, 42, 34, and 35.

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* *I.e.*, absolute or total representation.

† Excepting, of course, centres 27, 30 (see pp. 242 and 244).

(*c*) Rotation with adduction of head to the opposite shoulder. In a few instances we noted that the rotation of the head was scarcely so marked as a rolling over and adduction to the opposite shoulder. This action was observed at 46 and 48 only, thereby showing that it occurs very rarely as a primary movement. It will be seen later on that it was observed occasionally as a secondary movement along the lower border of the horizontal limb of the præcentral sulcus.

II. *Movements of the Eyes*

(*a*) Both eyes open. Before entering into the detailed account of the representation of this movement, we must observe that no great stress can with justice be laid on the frequency of the observation of this action; for the reason that unless the animal be very profoundly narcotised the eyes remain open, while on the other hand, if it be so deeply narcotised, the cortex is no longer excitable to the currents we employ. With this reservation, we will now discuss the frequency and position of its occurrence. Since we have obtained this movement of opening the eyes at almost every point in which turning of the head is represented, we are inclined to believe that this movement constantly occurs in association with that of the head, but, owing to the error of observation above referred to, we do not wish to speak more positively on this point. From two special experiments made to answer this question, we find that the movement was most represented at centre 32; from this point it diminished upwards and downwards, and especially in the former direction. With one doubtful exceptional case, the movement of opening the eyes is not represented along the middle line of the hemisphere or along the vertical line of centres immediately behind the sulcus *y*.

We are fortified in our opinion stated above by the fact that Professor FERRIER, in his work 'On the Functions of the Brain,' 2nd edit., p. 242, states that he obtained by stimulating his centre 12, which mainly corresponds to the region now under discussion, the following associated movements.—"the eyes open widely, the pupils dilate, and head and eyes turn to the opposite side."

(*b*) Both eyes turn horizontally to the opposite side. The eyes rarely turn to the opposite side as a primary movement; this action is best represented in the convolutions situated in front of the præcentral sulcus, and to a less degree behind the sulcus *y*. Just as the movement of opening the eyes is associated with that for rotation of the head, so in like manner the turning of the eyes is found in connection with the same movement of the head.

The further consideration of this movement is continued under the heading of "March," *vide* p. 213.

(*c*) Both eyes turn to the opposite side and upwards. This movement was very rarely observed, and only in centres 15, 16, 17, 19, 20, and very slightly at 33 and 31.

(*d*) Both eyes turn to opposite side and downwards. This movement was noticed but twice, and only at centre 22.

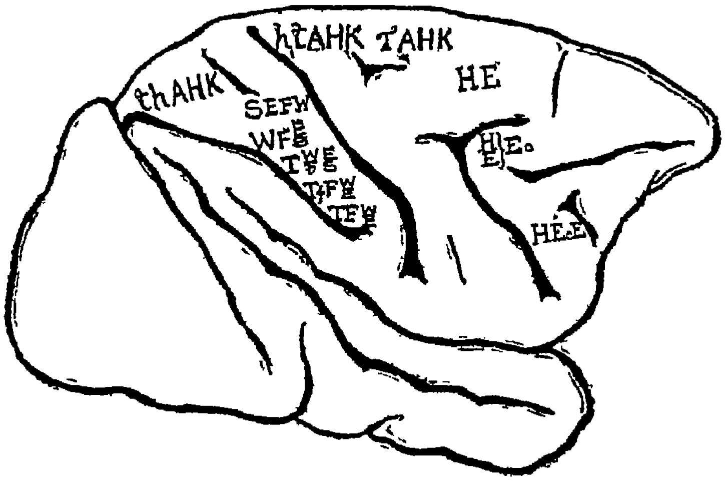
(*e*) Both eyes turn to the middle line, or only through a few degrees to the opposite side.

This action was observed to occur frequently in the centres 28, 28*a*, 26*a*, 26*b*. It consisted in a limited rotation of the eyes through a few degrees, such as would suffice to restore the direct position of the visual axes, if the eyes happened to be in position of slight conjugate deviation towards the hemisphere stimulated, and if any external strabismus happened to be present it was similarly instantly corrected.

In watching the rotation of the eyeballs we occasionally observed nystagmus of the eyes; this was only seen at the centres 15, 16, 29, and always consisted of rapid jerking movements towards the opposite side This was probably merely a result of fatigue.

III. *Movements of the Pupils.*—In the vast majority of instances there was no movement of the pupils; when it occurred dilatation was always noted. This dilatation of the pupils exists simply in association with turning of the head and eyes to the opposite side. It appeared to be represented most round the horizontal limb of the præcentral sulcus, but we did not observe it many times.

Fig 14



This figure is illustrative of the march or sequence of muscular spasm at those points in the areas investigated which appeared to be most constantly the seat of origin of such sequence The letters indicating the joints moved are placed in the order of the successive movements

A = Ankle
E = Eyes turning to opposite side
E*o* = Eyes opening
E = Elbow
F = All fingers
f = Index finger.
H = Head turning to opposite side.
H = Hip
h = Hallux
K = Knee.
S = Shoulder
T = Thumb
τ = All toes.
t = Small toes
W = Wrist

March or Sequence of Movement of the Head and Eyes. (See fig. 14.)

The relation of the movements of the turning of the head and eyes to the opposite side to that of opening the eyes varies as regards sequence of movement in the different parts of the cortex now under consideration. The sequence or order in which these movements occur forms the march for the part stimulated.

We shall take first the movements described above as an aid in dividing up the large area for the movements of the head and eyes, for the purpose of investigating the "March" It will be remembered that we postponed for later consideration the simultaneous movement of the head and eyes. The primary representation of this most important synergic action is given in Plate 40, fig. 5. It will be seen that its representation has a very wide distribution, which for the most part corresponds in mere extent with the representation of the movements of the head alone. As a primary movement, its importance entitles it to first consideration, for a review of the facts given in Table I.* will exhibit the very remarkable result that, of the 104 occasions on which this movement was observed to occur, in 100 instances it was primary. This is, no doubt, a demonstration of the necessity that this primitive movement should precede all others.

Taking first, then, the simultaneous movements of turning the head and eyes to the opposite side, the following march can be made out for a considerable number of centres. The order of this march is as follows —

1. Simultaneous turning of the head and eyes to the opposite side.
2. Opening of the eyes wide.
3. Continuation of turning of the head.

And this occurs at centres 14 to 17 inclusive and 34.

The part next to be considered is the region below the sulcus *w*, which extends downwards in front of the vertical limb of the præcentral sulcus. The following movements here form the march —

1. Turning of the head to the opposite side.
2. Opening of the eyes wide.
3. Turning of the eyes to the opposite side.

And are represented in the following centres, 19 to 28*b* inclusive. At the centres below *w* the opening of the eyes occurred earlier in the march than is just stated.

We would here direct special attention to the fact that occasionally the representation of the movements of the head and eyes is continued downwards, in front of the præcentral sulcus as far as its lower extremity, this area being limited in front by the subordinate sulcus (often very slightly marked) in the inferior frontal convolution, which probably represents the anterior limb of the Sylvian fissure.

We believe that it was owing to the very large proportion of negative results (*i.e.*, recorded nil) observed in stimulating this region, that Dr. FERRIER was led to consider it (*i.e.*, the part below the sulcus *w*) inexcitable.

We, however, find from a large number of observations that it is really excitable, although not invariably so. Of course, too, this excitability diminishes from above downwards. Not only is the representation in this region relatively less, but also the amount of movement evoked is much inferior in force and extent to that obtained in the centres above *w*.

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* See p. 242, *et seq.*

The relative amount of representation in the two parts is best shown by comparing the number of times in each in which no movement was obtained.

This will be made clearer by inspection of the following columns In the left side are set forth, in position corresponding to their arrangement in the cortex, the centres above and below the sulcus *w*, viz., all those below the horizontal limb of the præcentral sulcus. On the opposite side of the central line are correspondingly arranged fractions, the numerators of which denote the number of negative results obtained, while the denominators give the number of observations on each particular centre.

	CENTRES.			NILS.		
	14	15	16	$\frac{0}{19}$	$\frac{1}{19}$	$\frac{1}{19}$
	17	18	19	$\frac{1}{16}$	$\frac{3}{16}$	$\frac{6}{17}$
Level of *w*						
	22	26	27	$\frac{2}{18}$	$\frac{13}{18}$	$\frac{17}{18}$*
	24	26′		$\frac{3}{15}$	$\frac{6}{14}$	
	28	26*a*		$\frac{8}{18}$	$\frac{5}{16}$	
	28*a*	26*b*		$\frac{4}{16}$	$\frac{7}{16}$	
	28*b*	26*c*		$\frac{7}{13}$	$\frac{5}{11}$	
	28*c*	26*d*		$\frac{6}{9}$	$\frac{3}{5}$	

(The thick black line in each group of figures denotes the level of the sulcus *w*.)

To return to the existence of marked inferiority of functional activity of this region, we would repeat that this is the part of the head and eye area where excitation evokes rotation of the head and eyes through only a few degrees, such, for instance, as is requisite to direct the face to the middle line, if it be a little diverted towards the side stimulated.

In discussing the bearing of the less forcible character of the representation in this region as compared with that around the horizontal limb of the præcentral sulcus, it must be observed that the negative results occurred in Monkeys with small brains, in which case consequently this portion of the brain was only slightly developed.

PART V.—REPRESENTATION OF THE MOVEMENTS OF THE LOWER LIMB. (See figs 3, 6, 6A, 7, 8, 9, 10, 11, 12, 13, Plates 40 and 41.)

Before classifying and discussing the representation of the movements of the lower limb, it will be advisable to consider a few generalisations. In the first place, as we showed in our former paper, certain segments of the limb are of more importance than others; thus we demonstrated in the upper limb that its extremities, *i.e.*, the shoulder and the hand, possessed the greatest primary representation, the intermediate joints being only of subsidiary importance.

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* The one positive observation noted here was obtained in a Monkey in which the sulcus *w* was extremely short, so that centre 27 was brought near to the focus of representation

It is interesting to find that the same phenomenon is present in the lower limb, the foot and the hip taking the lion's share of primary movement, while the knee, the intermediate joint, occupies quite a subordinate position. Indeed, in many cases it was obvious that the movement of the knee was only consequential to that of the hip, thus mechanically relieving the tension necessarily produced by flexion of the former joint.

The differentiation of the movements of the lower limb is not nearly so minute and distinct as in the upper limb. This is extremely well exemplified in the mode of sequence of the movements of the segments in the two limbs. For instance, in the upper limb excitation of the middle of the ascending frontal convolution* produces a comparatively slow and orderly successive flexion of digits, wrist, elbow, and shoulder; whereas excitation of the same convolution above and behind the posterior extremity of x evokes rapid movement of all the toes, almost instantly followed by movement of the ankle and hip with, as before remarked, the subsequent and subordinate movement of the knee. Indeed the rapidity with which movement of one segment followed that of another was so great as to make it appear that each, with the exception of the knee, was represented equally in point of time. In this way it was frequently difficult to discover the exact march of the spasm produced even by minimal stimuli.

Hence the march and also, as will be subsequently shown in detail, the primary movement, both show the same character of the representation of the lower limb as is revealed in the performance of so-called volitional efforts. Whereas the upper limb performs movements of great complexity and speciality of purpose, those of the lower limb are engaged in actions of a lower grade which are far less individualised.

We now proceed to discuss the seat of primary movement in each segment of the lower limb, as we have observed such to occur, and in each instance also the character of the movements evoked at each point excited.

The segments of the lower limb may best be considered in the order from below upwards, inasmuch as the smallest segments possess the most extensive primary representation.

For accuracy and convenience it is necessary to refer to the movements of the toes, not only under the two headings of hallux and the rest of the toes respectively, which, for further convenience, we shall speak of as the small toes, but also to the movements of all the digits acting simultaneously as a whole, under the expression "all toes."

The movements of the segments will consequently be described in the following order:—

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* Centre 3, *vide* former paper.

Hallux,
All toes,
Small toes,
Ankle,
Knee,
Hip.

In describing the movements of each of these segments we shall give (i.) the total or *absolute* representation in each instance, (ii.) the *primary* representation, (iii.) the character of the movements comprising (*a*) the total or absolute representation of the part, and (*b*) the primary representation.

By the expression *total or absolute representation* of any segment, we mean that we have extracted from our records every single movement of each given segment at every one of our centres where that segment happened to be represented. The summation of these facts gives correctly the actual total amount of representation of each joint at each centre, and consequently tells us to what extent, as determined by electrical stimulation, that joint or segment is represented in the cerebral cortex.

The second heading under which we have classified our observations, viz., that of *primary representation*, requires little explanation, since, unlike the first heading just described, it defines the region in which any particular joint begins the general movement of the limb, excluding, of course, secondary, tertiary, or even quaternary representations of the segment of the limb, all these being included under the first heading.

The determination of the representation of the primary movement is of the greatest importance, since upon this rests the exact localisation of the starting point of epileptiform convulsions.

Finally, by the *character of the movement* we mean whether it be one of flexion, extension, &c., and this is separately considered, according as the movement is referable to (*a*) absolute or (*b*) primary representation.

REPRESENTATION OF THE HALLUX (see Plate 40, figs. 6, 6A).

(i.) *Total or Absolute Representation.*—The movements of the hallux are represented* at the following centres in order of diminishing frequency :—

$$71,\ \left\{\begin{matrix}69\\68\end{matrix}\right\},\ \left\{\begin{matrix}70\\62\end{matrix}\right\},\ \left\{\begin{matrix}61\\65\end{matrix}\right\},\ \left\{\begin{matrix}67\\64\\72\end{matrix}\right\},\ 59,\ \ 55\ \left\{\begin{matrix}54\\73\\75\\77\\6'\\6\end{matrix}\right\}\qquad\left\{\begin{matrix}58\\52\end{matrix}\right\}.$$

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* The centres enclosed vertically in brackets are those in which the degree of representation was equal.

On reference to Plate 40, figs 3 and 6, it will be seen that this is tantamount to saying that the hallux is frequently represented all over the area for the movements of the lower limb, with the exception of its hindermost extremity viz., centre 74. The maximum representation of the hallux is thus grouped round the upper end of the fissure of Rolando, and by reference to Table I, p. 250, &c, and fig 6 it is evident that the representation of this segment decreases rapidly in intensity posteriorly, but more gradually anteriorly and inferiorly, reaching a minimum at each end of the lower limb area (*cf.* the region for absolute representation of "all toes"). The total number of times that the hallux was observed to move was 138.

(ii.) *Primary Representation* (see fig. 6A).—The hallux is primarily represented at

69, 68, 71, 62, 70, 61, 67, 65, 72, 75, 59, 58,

the centres being here arranged in order of decreasing intensity of representation.

It occurred to us that the order of these centres of primary representation ought to be decided by different considerations to those by which were determined the relative positions of the centres of *total* representation. Consequently we have gauged the intensity of the *primary* representation, not only by the greater proportionate[*] frequency with which it actually occurred, but also by its being accompanied or not by the occasional primary representation of other segments, *e g*, the small toes.

It will thus be seen that the hallux is represented in primary movement in a very large proportion of the centres which are relegated to the movements of the lower limb, in fact it occurs primarily in the proportion of over 50 per cent. While noting that the hallux is represented as a primary movement to such a degree, it is important to remember that its chief region of primary representation is close around the upper end of the fissure of Rolando. This latter generalisation not only assumes special importance in connection with the diagnosis of the seat of disturbance in an epileptiform convulsion beginning in the hallux, but also because it points to the fact, upon which stress will later be laid, that this part is the focal region of the representation of the lower limb. A total number of 82 primary movements of the hallux were observed.

III. *Character of Movement.*—(*a.*) *Absolute.* (*b*) *Primary.*

We have found, somewhat unexpectedly, that there is no distinct localisation of any particular movement; extension and flexion[†] being apparently equally represented in any centre for movement of the hallux. It is true that there is a slight difference, according as the movement is a primary movement or not; thus we find that out of 82 instances of primary movement of the hallux, 47 were flexion adduction and opposition, i.e., mainly flexion, while only 35 were the converse, viz., extension abduction.

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[*] By "proportionate" we mean the ratio of the primary movement of the hallux to all other primary movements occurring at the same segment (see p 220, "Primary Representation of All Toes").

[†] In employing the term flexion of the hallux we have found it advisable to include therein not only direct flexion but also the more specialised movements of adduction and opposition. Although in this species of Monkey the hallux is employed as a thumb, nevertheless the special movements just mentioned were so frequently accompanied by the action of flexion, that the representation was most accurately described as that of flexion into the sole.

When, however, we come to enumerate the total or absolute number of instances in which the hallux moved, we find that this relationship is reversed, and that extension distinctly predominates. For instance, if we take the focus of representation of the hallux, viz., centres 69,71, and summate the absolute representation of movements, we find that "extension" occurs fifteen times, whereas "flexion" was observed only 6 times. Flexion is primarily represented at

$$70,\ \left\{\begin{matrix}69\\71\end{matrix}\right\},\ \left\{\begin{matrix}68\\67\end{matrix}\right\},\ \left\{\begin{matrix}61\\62\\72\end{matrix}\right\},\ \left\{\begin{matrix}65\\75\\59\end{matrix}\right\},\ 58$$

while on the other hand extension is represented at

$$\left\{\begin{matrix}69\\62\\71\end{matrix}\right\},\ 61,\ 65,\ \left\{\begin{matrix}67\\72\\75\\77\end{matrix}\right\},\ \left\{\begin{matrix}70\\58\end{matrix}\right\}$$

Hence, although flexion is the more frequent *primary* movement of the hallux, extension is the more important from an *absolute* point of view.

In our previous paper we drew attention to the combination of these movements as affecting the fingers, but in the lower limb it is most interesting to note that we have only observed extension of the hallux followed by flexion in one instance, viz., in Monkey 38, centre 64, where slight extension of the hallux preceded flexion. In connection with this it is proper to state that in Monkey 40 we thrice observed, viz., at centres 59, 61, 62, that adduction of the hallux was preceded by a slight movement of extension. The converse combination of these two exists, which merits attention, viz., the antecedence of extension by flexion—the movement of flexion being slight, and being instantly followed by a more powerful and permanent extension. When it is taken into account that the exceptional instances of flexion being preceded by extension are the only ones of the kind out of 138 recorded movements of the hallux, it is clear that some very remarkable relation exists between these two fundamental movements of this segment, though hitherto we have failed to discover any reason why the one combination should exist to the exclusion of the other—*cf.* representation of movement of toes, p. 222.

Representation of Movements of All Toes, acting simultaneously.

(See Plate 40, fig. 7.)

(i.) *Total or Absolute Representation.*—The movement of all toes occurs at the following centres, in order of diminishing intensity,

$$71,\ 68,\ \left\{\begin{matrix}67\\58\end{matrix}\right\},\ \left\{\begin{matrix}69\\65\\61\end{matrix}\right\},\ \left\{\begin{matrix}73\\76\\77\\64\\54\end{matrix}\right\},\ \left\{\begin{matrix}62\\59\\52\end{matrix}\right\},\ \left\{\begin{matrix}72\\70\end{matrix}\right\},\ \left\{\begin{matrix}75\\6\end{matrix}\right\},\ 74,\ 6',\ 55.$$

Although we here give a list of the localities at which we have observed combined simultaneous movement of all the toes, we wish most particularly to remark that, on *a priori* grounds, it is not to be expected that such simultaneous movements should be as constantly localised as those of a highly specialised segment, like the hallux; further, we wish to draw attention to the fact that it may well happen that occasionally in those localities where the movement of the toes succeeds that of the hallux the time-interval may be so short that the movements are practically synchronous. For example, we have several times obtained, first, synchronous movements of all the digits; and, later, by carefully repeated minimal stimulation, discovered that occasionally there was a distinct interval between the movement of the hallux and the rest of the digits. It might have seemed justifiable to ignore those instances where the time-interval was exceedingly short, but we have thought it more accurate to record all the movements exactly as they occurred.

(ii.) *Primary Representation* of "all toes" occurs in diminishing intensity at centres,

$$77,\ 74,\ \left\{\begin{matrix}58\\52\end{matrix}\right\},\ 73,\ 54,\ 64,\ \left\{\begin{matrix}61\\67\end{matrix}\right\},\ 59,\ \left\{\begin{matrix}65\\72\\71\\76\end{matrix}\right\},\ 68,\ 70,\ 69.$$

We have drawn up the above list, as in the case of the hallux, according to the degree of intensity of the primary representation of "all toes" at any given centre.

This intensity has been estimated by taking the proportion of the primary representation of "all toes" as compared with frequency of occurrence of movement of other segments of the lower limb; these proportionate numbers have furnished the indices for each centre

This order reveals a very definite symmetrical arrangement, not only constant as regards the position of the representation of all toes, but also with reference to the primary representation of the hallux. This latter, it will be remembered (see page 218), was grouped in greatest intensity round the upper end of the fissure of ROLANDO, this being the middle third of the lower limb area. In striking contrast to this (*cf.* figs. 6 and 7), we find that the representation of "all toes" is grouped at each extremity of the lower limb area, from which points it gradually diminishes in intensity towards the focus of representation for the hallux. Now, the hindermost centres of the lower limb area being 77 and 74, whereas 52 and 58 are the most anterior; these four centres are seen to head the above list of the primary representation of "all toes," showing that in the combination of the hallux and small toes forming the group of all toes, it is the smaller digits which take the larger share of the primary representation. Primary movement of "all toes" was observed 78 times.

(iii.) *Character of Movements.*

(*a*) *Absolute*—The first point of interest to be noted in the character of movements of "all toes" is that to which we drew attention, in discussing those of the hallux (p. 219), viz., that extension is the more frequent movement. Thus, out of 138 simultaneous movements of "all toes," only 21 were flexion, all the rest being extension. But a still more remarkable fact is brought out in considering the localities where these two opposite movements are represented; we have just seen that the simultaneous movement of "all toes" is most represented in positions exactly complementary to that of the hallux, it is now interesting to observe that the most important movement of the digits, *i e*, extension, is characteristic of the chief foci of representation of "all toes," while the far rarer movement of flexion is only to be found in those centres where the primary representation of "all toes" is overshadowed by that of the hallux.

The centres where flexion was most observed (arranged in successive order of decreasing importance) were —

$$\left\{\begin{matrix} 69 \\ 68 \\ 64 \end{matrix}\right\}, \quad \left\{\begin{matrix} 6 \\ 76 \\ 58 \\ 67 \end{matrix}\right\}, \quad \left\{\begin{matrix} 70 \\ 71 \\ 65 \\ 61 \end{matrix}\right\}.$$

Comparison of figs. 6A and 8 with fig 10 will show still more clearly than this list the relative position of the proportionate frequency of flexion.

(*b.*) *Primary.*—The character of the primary movement of "all toes" corresponds so closely with that of the absolute movement that it need not be separately considered.

Representation of Movements of Small Toes. (See fig. 10.)

(i.) *Total or Absolute Representation.*—Movements of the small toes we have observed to occur on excitation of the following centres, in order of decreasing intensity:—

$$62, \quad 65, \quad \left\{\begin{matrix} 69 \\ 67 \end{matrix}\right\}, \quad 64, \quad \begin{matrix} 55 \\ 59 \\ 68 \\ 70 \\ 72 \\ 73 \end{matrix} \quad \left\{\begin{matrix} 78 \\ 6' \end{matrix}\right\}, \quad 61, \quad < \begin{matrix} 54 \\ 74 \\ 75 \\ 76 \\ 77 \\ 6 \end{matrix}$$

On referring to Table I. for further details of this list, it is apparent how much less frequently the movement of small toes is represented than that of "all toes" or hallux, the figures being respectively 92, 138, and 138.

(ii.) *Primary Representation.*—The intensity of primary representation is given in the following order :—

$$78,\ 55,\ 64,\ \begin{Bmatrix}62\\72\end{Bmatrix},\ 67,\ 65,\ 73,\ 74,\ 6',\ 77,\ 6,\ 70,\ 76,\ 69.$$

Owing to the comparative rarity with which primary movement of "small toes" occurs, it is necessary to be cautious in forming generalisations from this list, but it is abundantly clear that the fundamentally important generalisation which was so obviously true for the movements of all toes, also applies in the case of the small toes, viz., that the representation of the small toes is complementary to that of the hallux. For not only does movement of the small toes occur primarily but once at centre 69, and but twice at 70, where other primary movements occur to the number of 14 and 16 respectively, but also the "small toes," as such, are not so represented at 68 and 71. Primary movement of the small toes was noted 44 times.

At the same time it is evident, from the general rarity of primary movement of the small toes, that it is of very inferior importance among the movements of the lower limb. This conclusion is completely confirmed by observation of the so-called voluntary movements of the toes; primary simultaneous action of the small toes being extremely rare, and, perhaps, scarcely ever performed by Man, or by this species of Monkey.

(iii.) *Character of Movement.*

(*a.*) *Absolute.*—Again we find that, as in the case of "all toes," the movement of extension is much more largely represented than that of flexion. Thus, out of a total of 92 movements, 78 were extension and 14 flexion.

A further point of material interest in connection with this remarkable preponderance of the movement of extension is to be seen in the fact that the movement of flexion, when it happened, was observed only at centres

$$67,\ \begin{Bmatrix}68\\62\end{Bmatrix},\ 69,\ 64,\ 54,\ 6';$$

these, with one exception, form a group immediately in front of the fissure of ROLANDO, and in the same region which we have already seen in the case of "all toes" to be connected especially with the flexion movements of those digits as well as the general representation of the hallux.

As we shall now leave the consideration of the movements of the toes for that of the movements of the ankle, it seems to us very desirable to make further reference to the fact just mentioned, viz., the peculiar localisation of the rare movement of flexion of the small toes in what we may call the hallux region of the lower limb area.

To put the matter in a simpler light than is offered by the bare record of observations, let us state again that the whole region of representation of the lower limb is a narrow strip running along and forming the upper fifth of the convex outer surface of the excitable region in the hemisphere; further, that the middle of this strip, or more strictly speaking, the junction of its middle and posterior thirds, is essentially the seat of representation of the hallux, while each extremity is essentially the seat of representation of the small toes.

To continue the commonest primary movement of the hallux differs from that of the small toes in being flexion for the former and extension for the latter. Consequently we may say that, other things being equal, the movement of flexion will be characteristic of the more central portion of the lower limb area, while extension will be more marked at each extremity of this part. Under these circumstances it seems to us justifiable to entertain the belief that possibly a movement which is characteristic of any given segment in its focus of representation may be overshadowed by a different movement, if the representation of that segment is carried (diminishing in intensity, of course) into the focal region of some other segment whose characteristic movement is of an opposite nature. To be more particular, we would suggest then that this is the reason why flexion of the small toes is observed more frequently as the representation of those digits (whose characteristic primary movement is extension) invades, as it were, the region of the hallux (whose characteristic primary movement is flexion). We do not wish to press this point unduly, for the reason that the actual number of times that flexion of the small toes occurred is not large, but, as will be seen on reference to figs. 6, 8, and 9, the existence of this remarkable relation between the representation of flexion and extension in the toes is undeniable.

REPRESENTATION OF THE MOVEMENTS OF THE ANKLE (Plate 41, fig. 11).

(i.) *Total or Absolute Representation.*—Movement of the ankle occurs in order of decreasing frequency at the centres—

$$68, 61, \begin{Bmatrix} 65 \\ 72 \end{Bmatrix}, \begin{Bmatrix} 62 \\ 67 \\ 70 \\ 71 \end{Bmatrix}, \begin{Bmatrix} 59 \\ 76 \end{Bmatrix}, \begin{Bmatrix} 69 \\ 73 \end{Bmatrix}, \begin{Bmatrix} 58 \\ 64 \\ 6' \end{Bmatrix}, \begin{Bmatrix} 55 \\ 77 \end{Bmatrix}, 54, 75, \begin{Bmatrix} 52 \\ 78 \\ 6 \end{Bmatrix}, \begin{Bmatrix} 51 \\ 74 \end{Bmatrix}, 80.$$

On comparing these numbers with fig. 1, it is clear that the ankle is not specially represented in any one portion of the lower limb area, its focus only being situated in the centre of the area, and its intensity decreasing towards the borders with that of the limb generally.

The total number of times that we observed movement of the ankle was 198, a number which, as might have been expected, owing to the relative position of the joint in the limb, is far in excess of that of any other part.

(ii.) *Primary Representation.*—In marked contrast to the segments already described, primary representation of the ankle is of rare occurence, being observed only 36 times out of 198 actual movements Although occurring so rarely, it is nevertheless important to remark that it was observed at no less than two-thirds (16 out of 23) of the centres in the lower limb area, thus again showing the general and subordinate character of the representation of this joint as compared with the focal character of that of others.

The infrequency of occurrence of primary movement of this joint diminishes, of course, the value of any arrangement in order of intensity of the same, and therefore we shall do no more now than state the arrangement we have found—

$$62,\ 59,\ 68,\ 74,\ \begin{Bmatrix}58\\61\end{Bmatrix},\ \begin{Bmatrix}70\\72\end{Bmatrix},\ \begin{Bmatrix}64\\69\\73\end{Bmatrix},\ 77,\ \begin{Bmatrix}71\\76\end{Bmatrix},\ 75,\ 6.$$

(iii.) *Character of Movement*—(*a*) *Absolute.*—The movements of the ankle are:—

(a.) *Dorsal flexion.* (By this we mean what is frequently called *flexion* of the joint, *i.e*, when the toes are brought upwards, so as to approach to the front of the leg.)

(b.) *Plantar extension.* (By this we mean the opposite to dorsal flexion, *i.e*, when the toes are pointed downwards, the heel being drawn upwards. This movement is frequently called *extension* of the ankle)

NOTE.—We have preferred to employ these arbitrary terms as conveying a distinct notion of the direction in which the foot moves, thus, at the same time avoiding the homologically false use of the simple terms flexion and extension.

(c.) *Eversion.*

(d.) *Inversion.*

These movements (of an absolute total of 198) occurred in the following order of frequency:—

Dorsal flexion	116 times
Eversion	31 „
Plantar extension . . .	26 „
Inversion	21 „

Confusion between dorsal flexion and plantar extension was noted in four instances.

The analysis of the localisation of the movements of dorsal flexion and plantar extension respectively gives no further information than that dorsal flexion is represented in proportion to the amount of general representation of the limb as a whole. Further that, apparently for the same reason, plantar extension was only observed in the middle of the lower limb area, especially since that part, as we have just shown, is essentially the region of representation of true, *i.e.*, homologous, flexion rather than of extension.

The movements of eversion and inversion deserve a passing notice. Their distribution in the lower limb area appears to be guided only by the relative degree of representation of the limb in the various parts of its cortical area.

In examining the question as to whether there exists any correlation between dorsal flexion and plantar extension, on the one hand, and eversion and inversion, on the other, we have found that the synergic relation between these movements was no more than the simple relation of probable frequency in proportion to the amount of actual representation of each. Hence it is impossible to make any generalisations on this point.

(*b*) *Primary Movement*—The number of times that primary movement was observed was 36. Of this number,

Dorsal flexion occurred . .	14 times
Eversion „ .	12 „
Plantar extension „	8 „
Inversion „	2 „

Beyond the obviously altered relation in the degree of representation which these movements bear to one another when primarily represented and when arranged in the order of the number of total representation, *i e*, all movements observed, there is nothing further to be remarked upon this point, save to mention that this small degree of primary representation is found, as might be expected, just in the middle of the lower limb area, *i.e.*, around and especially in front of the upper part of the fissure of ROLANDO.

REPRESENTATION OF THE MOVEMENTS OF THE KNEE (Plate 41, fig. 12)

(i.) *Total or Absolute Representation.*—Movement of the knee occurs in order of decreasing frequency at the centres :—

$$\begin{Bmatrix}65\\68\end{Bmatrix}, \begin{Bmatrix}67\\71\end{Bmatrix}, 70, \begin{Bmatrix}54\\69\\73\\6'\end{Bmatrix}, \begin{Bmatrix}55\\64\end{Bmatrix}, \begin{Bmatrix}61\\62\end{Bmatrix}, \begin{Bmatrix}72\\77\end{Bmatrix}, \begin{Bmatrix}75\\76\\59\\6\end{Bmatrix}, 58, \begin{Bmatrix}52\\74\\98\end{Bmatrix}.$$

The knee is thus represented all over the entire lower limb area, the total number of movements observed being 141 (*cf.* Ankle).

Further on we shall draw attention to the fact that the movements of the knee are essentially dependent upon those of the hip.

(ii.) *Primary Representation*—The knee we have observed to move primarily only ten times, *i.e.* $\frac{1}{27}$th of the total primary movements of all the segments of the lower limb. And, moreover, of these ten times, in four it was associated with other synergic primary movements, *i.e.*, of hip and other joints. Consequently its *rôle* as a joint of primary movement is most insignificant, and we shall return to this question in discussing the representation of "purposive" actions of the limb.

(iii.) *Character of Movement.*—(a) *Absolute* —Of the total number of movements observed,

Flexion occurred . . .	118 times
Extension „ . . .	12 „
Rotation in „ .	7 „

and confusion was noted in four instances.

The movement of extension, it is important to observe, occurred at the following centres in order of frequency :—

$$6, \left\{\begin{matrix}55\\61\end{matrix}\right. \quad \left\{\begin{matrix}54\\68\\69\\75\end{matrix}\right\},$$

and hence, though rare, it is represented about the same region as is the equally rare movement of flexion of the small toes, *i.e.*, close to the fissure of ROLANDO This, as we have pointed out before, is the focus of representation of the limb, and perhaps the rare movements of extension and rotation in, which occur at the centres :—

$$68, \left\{\begin{matrix}6'\\6\\69\\70\\73\end{matrix}\right\},$$

owe their representation to the fact that, this being the middle of the lower limb area, the cortex here is most highly organised, and thus possesses centres for every movement of all the joints.

(b.) *Primary.*—The 10 primary movements of the knee were all flexion, with one exception, viz., rotation in.

REPRESENTATION OF THE MOVEMENTS OF THE HIP (see Plate 41, fig. 13).

(i) *Total or Absolute Representation.*—Movement of the hip occurs in order of decreasing frequency at the centres :—

$$67, \left\{\begin{matrix}65\\6\end{matrix}\right\}, \left\{\begin{matrix}61\\68\\71\end{matrix}\right\}, \left\{\begin{matrix}55\\70\end{matrix}\right\}, \left\{\begin{matrix}54\\62\\64\\73\\6'\end{matrix}\right\}, \left\{\begin{matrix}59\\69\\72\\75\\76\end{matrix}\right\}, 77, 58, 52, \left\{\begin{matrix}74\\78\end{matrix}\right\}.$$

The hip is thus represented most in the middle or focus of the lower limb area, moving altogether 177 times.

(ii.) *Primary Representation.*—The hip is primarily represented in the following centres in order of diminishing intensity.—

$$54, 76, 75, \left\{\begin{matrix} 6' \\ 6 \end{matrix}\right\}, 55, \left\{\begin{matrix} 64 \\ 65 \end{matrix}\right\}, 52, 59, 61.$$

We must first call attention to the important deduction which these figures reveal, namely, that the hip is *primarily* represented in but 11 out of the 23 centres of its total or absolute representation, further that the centres, where it was observed to move primarily, are exactly the counterpart of those where the hallux is especially primarily represented. In accordance with the same fact, it is to be noted that behind the fissure of Rolando the hip is only represented in two centres, viz, 76 and 75, and that these centres are situated at the lower border of the area of representation of the limb. This localisation of the hip to the lower border of the area is equally strongly marked in front of the fissure of Rolando, and culminates in the fact that the centre in which most primary representation of the hip was found to occur is the lowest and most anterior of the whole lower limb group, viz., centre 54.* Primary movement of the hip was observed only 27 times.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of 177 movements,

Flexion occurred		118	times
Rotation out	,,	35	,,
Extension	,,	23	,,
Confusion	,,	4	,,
Abduction	,,	2	,,
Rotation in	,,	1	,,

Extension, remarkably rare in occurrence, was observed at the following centres in order of decreasing frequency—

$$6,\ 6',\ \left\{\begin{matrix} 55 \\ 61 \\ 75 \end{matrix}\right\},\ \left\{\begin{matrix} 52 \\ 64 \\ 62 \\ 69 \\ 72 \end{matrix}\right\}.$$

It is evident from these figures that this infrequent movement is most represented in the neighbourhood of centre 6, both behind and in front of the fissure of Rolando.

Rotation out occurs at centres:—

---

* Here we should remark that centre 51, although a border centre, where various parts of the body are represented (see p. 238), is also a centre where the hip is notably represented in primary movement (see also Table I.)

$$68,\ 59,\ \begin{Bmatrix}65\\67\end{Bmatrix},\ \begin{Bmatrix}55\\61\end{Bmatrix},\ 70,\ \begin{Bmatrix}52\\58\\64\\72\\76\\6'\end{Bmatrix}.$$

But there does not seem to be any definite localisation of the movements.

(b.) *Primary.*—Of the 27 primary movements :—

12 were flexion,
10 ,, extension,
5 ,, rotation out

Flexion as a primary movement was most marked at 54 (6 times), then at 76 (twice), 59, 64, 6′, 75.

Extension was most marked at 6, then 75, 52, 61, 64, 61′.

Although so seldom moving primarily, it is interesting to note that when this did occur, the hip was nearly as often extended as flexed; while on the other hand, as noted above, in the movements of the joint of secondary, tertiary, and quaternary sequence, extension was extremely rare as compared to flexion.

MARCH OR SEQUENCE OF MOVEMENTS IN THE SEGMENTS OF THE LOWER LIMB.

(See fig. 14, p. 213.)

The sequence of movements successively invading the various segments of the limb, when any given point in the cortex is excited, varies in mode according to the segment in which the movement commences. For this reason the facts are best grouped together according to the seat of the primary movement. Thus we have different types named after the various segments of the limb. We commence with the most frequent.

Class I.—*Hallux Type*, observed at centres 61, 62, 65, 67, 68, 69, 70, 71, 72.

The march of the muscular spasm when commencing with movement of the hallux is very constant, the order of joints affected being almost invariably :—

Hallux, *Small Toes*, *Ankle*, *Hip*, and *Knee*.

In a relatively considerable number of instances the hip and knee moved simultaneously, and in one the movement of the knee preceded that of the hip.

The character of movement in the march was as follows :—

Hallux $\begin{Bmatrix}\text{flexed*}\\ \text{or}\\ \text{extended}\end{Bmatrix}$; *Small Toes* extended; *Ankle* dorsally flexed; *Hip* flexed; *Knee* flexed.

---

* Flexion more frequently than extension (see p. 210).

The general effect produced was thus, of course, a drawing up of the limb with extension of the digits The movement of flexion of the knee might thereby gain a fictitious importance, if we did not at this moment explain that it was very frequently simply secondary to, and necessitated by, the flexion of the hip. It has already been pointed out what a very subordinate position the knee occupies among the joints of the limb, and especially that it is practically never primarily represented

Class II.—"*All Toes*" *Type*, observed at centres 64, 58, 59, 72, 52, 54, 73, 77.

The character of the movement and the order was —

All Toes extend, *Ankle* dorsally flexed; *Hip* flexed; *Knee* flexed.

At each of the three last centres mentioned above there was once presented a slight variation in the order of the march; but, being so infrequent, these variations were not deemed sufficiently important to merit separate description.

Class III.—"*Small Toes*" *Type*, observed at 55, 64, 78.

This type, only occurring three times, presents considerable confusion of arrangement, which deprives it of much importance. The localisation of the commencement of the march was fairly constant, viz, movement of the small toes, followed by that of the hallux. Consequent on the movement of the hallux we should naturally have expected movement of the ankle, and then of the hip and knee. At centres 64 and 78 this was indeed the case, but at centre 55 movement of the ankle terminated the march.

It will be remembered that in a few, comparatively rare, instances the ankle, knee, and hip commenced movement in the limb. It appeared to us likely that some interesting facts might be obtained by analysing these exceptional cases. This we did, and the results are best arrived at in the following order —

(*a.*) *Ankle Type* —The study of the march, when the movement is begun by the ankle, gave the following order, which was fairly constant, viz.—

Ankle, Toes, Hip, Knee

(*b*) *Knee Type.*—Similarly, summation of the instances when the primary movement began in the knee was productive of the following result, as the most usual order of the march, viz :—

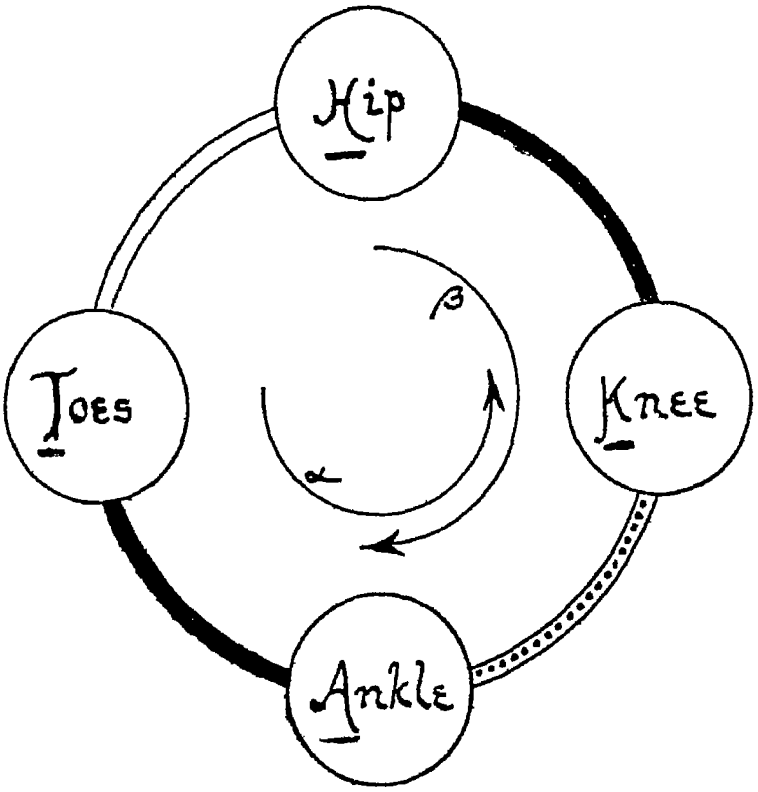
Knee, Hip, Ankle, Toes.

(*c.*) *The Hip Type.*—The commonest order of movement in this type was found to be .—

Hip, Knee, Ankle, Toes.

Comparison of arrangement in each of these more unusual marches with that of the common types described on pp 228, 229 seems to us to suggest that the mechanism of a cortical motor centre is almost constant in arrangement, and that for the lower limb it may schematically be represented thus (fig. 15).

Fig 15.



In this schematic figure the lines connecting the limb segments are made dark, dotted, or white to show the difference in amount or degree of association existing between the representation of the knee and hips, and between that of the ankle and toes respectively. (It must not be forgotten that this association is not only psychical in origin, but is also conditioned by the anatomical configuration of the muscles moving the various segments, whereby it happens, for example, that the hip cannot be notably flexed without similar movement of the knee, and again, that the powerful flexion of the toes causes plantar extension of the foot.)

Now the flow of energy which most frequently follows excitation is from T along the direction of the arrow α to H, but occasionally it is in the reverse direction, from H along the direction of the arrow β to T. This simple reversion of the current Dr. Hughlings Jackson fully described many years ago, as occurring in disease of the cortex in Man, and therefore we need not further consider it here. But, as we have just stated, in certain exceptional cases the flow of energy may start from A or from K. Of these two A is by far the more important, the movements of the knee being so very largely conditioned by those of the hip. Now, when the initial spasm affects the ankle, it is clear from the order in the ankle type of march that the energy flows in the more unusual direction of the arrow β, and so really simply continues the hip type of march. This mode of regarding the ankle type of march is of value as enabling us without exaggeration to harmonise what might otherwise appear to be conflicting observations.

Moreover, the *Knee Type* also probably conforms to the same system, although the order, viz., K, H, A, T seems at first sight to be wholly exceptional. The explanation of this may possibly be that the movements of the knee are so dependent on those of the hips as to bring their seats of representation in far closer connection than the union of the knee division of the area with its other neighbour (anatomically and schematically speaking) the ankle division. Hence, given the movement commencing in K, the course it will theoretically, and actually as observed by experiment, take is K, H, A, T, and not K, A, T, H.

PART VI.—REPRESENTATION OF THE MOVEMENTS OF THE UPPER LIMB

In our former Paper in the 'Philosophical Transactions,' *loc. cit.*, we considered the representation of the upper limb as it occurred in the anterior half of the ascending parietal convolution. In the present paper we supplement our former account by a description of the movements obtained when the posterior half of that convolution is stimulated.

It will be useful if we now give in their positions the figures indicating the centres into which we divided the anterior half of the middle two-fourths of the ascending parietal convolution in our previous paper, and those of the posterior half adopted in the present research—

80	79	11
82	81	9
	83	8′
	85	8
	87	7′
		7

Above 80, 79, 11 is the parietal lobule. (See also fig. 2.)

In our former paper we contented ourselves with describing in one table the primary movement, the march, and the character of all the movements obtained. In the present instance, however, we shall follow the more minute arrangement adopted in the foregoing pages.

We shall now describe the movements of the various segments in the order of thumb, fingers, wrist, elbow, shoulder.

Representation of the Movements of the Thumb.

(See fig. 16, which with figs. 17, 18, 19, and 20 are extensions of the diagrams of the representation of the upper limb segments given in our former paper).

(i.) *Total or Absolute Representation.*—The thumb is represented along the posterior part of the ascending parietal convolution in the lowest four centres only, as follows, commencing with the most important, 87, 85, 83, 81

The total number of times movement was observed was 40 (39 at centres 87, 85, 83).

(ii.) *Primary Movement.*—The thumb moved primarily at centres 87, 85, 83. It is most essential that we should here point out that at centre 87 not only did every movement of the thumb occur as a primary movement, but also that no other segment of the limb participated in such primary movement. It is further to be remarked that at centres 85 and 83 the primary movements almost equalled in number the absolute representation. (See Table I, p 252.)

(iii.) *Character of the Movements.*—(a) *Absolute.*—Of the 40 movements of the thumb,

26 were flexion and
14 „ opposition.

Consequently the *general* movement of flexion of the digit into the palm was the only movement obtained.

(b.) *Primary.*—Of 37 movements,

25 were flexion and
12 „ opposition.

These facts, coupled with those we noted in our previous paper, leave it beyond doubt that this region, viz., the middle third of the ascending parietal convolution, is the focus of representation of the movements of the thumb.

REPRESENTATION OF THE MOVEMENTS OF THE FINGERS (See Plate 42, fig. 17).

(i.) *Total or Absolute Representation.*—The fingers are represented, in order of diminishing intensity, at the centres —

$$85, 83, 87, 82, 11, \left\{\begin{matrix}79\\80\\81\\6\end{matrix}\right\}, 6'.$$

It is worthy of remark that at 85 the representation of the fingers was found to be present 15 times, in contrast to 8 times at 87 and 7 times at 83.

The total number of movements observed was 54.

(ii.) *Primary Representation.*—Primary movement of the fingers was observed at the following centres, in order as before:—

82, 85, 83, 81.*

On close scrutiny we found that at centre 85 the index finger was primarily represented no less than 4 times in association with the thumb. The chiefest representation of the fingers all moving together is centralised at 82. Thus there exists, as might have been surmised, a gradation from above down of primary representation of all fingers, index, and thumb at the centres 82, 85, and 87 respectively.

---

* Note complete absence of primary representation of the fingers at centre 87.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of the total number of 54 movements,

35 were flexion,
15 „ extension,
4 „ "interosseal position."

At centre 85, where the greatest number of movements occurred, of 15 observations flexion occurred 14 times. And at 87 also flexion was alone obtained.

In striking contrast to this representation of flexion at the lowest part of this region, we find the movement of extension is alone represented at the highest part of the region, viz., at centres 11 and 79. In front of the fissure of ROLANDO, a somewhat different arrangement prevails at the upper part of the upper limb area. Here, as we showed in our previous paper, movement of the fingers occurred very slightly in degree and very late in time, and the character of this late and feeble movement was flexion. This fact we have now confirmed in our re-examination of the border centres 6 and 6′ (situated between the upper and lower limb centres).

(b.) *Primary.*—Of 11 movements,

4 were flexion,
3 „ extension,
4 „ abduction of the index.

The rarity of primary movement of the fingers here indicated is explicable by the fact that in the ascending parietal gyrus the movements of the fingers are almost universally secondary to those of the thumb. Thus of fifteen absolute movements of the "all fingers" (*i.e.*, excluding primary movements of the index), only 1 was a primary movement, and that was associated with the thumb. Reference also to the plate in our former paper and to fig. 14 shows this important preponderating influence of the thumb.

REPRESENTATION OF THE MOVEMENTS OF THE WRIST. (See fig. 18.)

(i.) *Total or Absolute Representation.*—The movements of the wrist are represented in the following centres, arranged in order as before:—

$$83,\ 85,\ \left\{\begin{matrix}87\\82\end{matrix}\right\},\ \left\{\begin{matrix}81\\80\\11\\6\end{matrix}\right\},\ \left\{\begin{matrix}79\\6'\end{matrix}\right\}$$

The total number of movements observed was 40.

(ii.) *Primary Representation.*—The wrist initiated movement of the limb at the following centres :—

$$\left\{\begin{matrix}80\\81\\82\end{matrix}\right\}, 83, 6', 85, \left\{\begin{matrix}11\\79\end{matrix}\right\}, 6.$$

Altogether 16 movements were observed. The universality of representation of this joint in nearly all* the centres for the upper limb now under consideration, again demonstrates the condition described in our former paper, viz., that this joint is subordinate to the movements of the other segments of the limb, and notably to those of the digits.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of the 40 movements observed, no less than

21 were pronation,
14 ,, extension,
4 ,, supination,
1 was ulnar adduction.

Thus, while in no case was flexion observed, it is most noteworthy that pronation was the commonest movement. We would like again to quote the opinion expressed in our former paper as to the important part played by the movement of extension of the wrist in fixing the hand as a prefatory procedure in delicate movements of the digits, but we would insist that, even more than extension, pronation is absolutely essential to the correct performance of accurate and minute movements of the thumb and forefinger, the most highly specialised of the fingers. We therefore find the wrist represented immediately above (*i.e.*, preceding functionally) the areas for the latter segments. The movement of supination was noted at centres 87 and 85, but nowhere else, and occurred at the end of the act (*vide* March, *infra*).

(b.) *Primary.*—Of a total of 16 primary movements every one was pronation (*vide* March).

The intensity or degree of representation of this movement corresponds to the order given in (ii.) that of the primary representation of the joint.

REPRESENTATION OF THE MOVEMENTS OF THE ELBOW. (See Plate 42, fig. 19.)

(i.) *Total or Absolute Representation.*—The movements of the elbow are represented at the following centres, arranged in order of decreasing intensity :—

$$6, 11, 79, 6', 83, \left\{\begin{matrix}81\\82\\85\end{matrix}\right\}, \left\{\begin{matrix}80\\87\end{matrix}\right\}.$$

The total number of movements observed was 50.

---

* Nine out of ten.

(ii.) *Primary Representation.*—The elbow initiated the movements of the limb in 9 instances at 7 centres :—

$$80, \left\{\begin{matrix}81\\82\end{matrix}\right\}, 6, 6', 11, 83.$$

Proportionately we thus see that the elbow is very generally though feebly primarily represented (*cf* the Wrist)

(iii.) *Character of Movement.* (a.) *Absolute.*—Of the 50 movements,

26 were extension,
23 „ flexion,
1 was confusion.

These opposed movements were grouped thus: extension alone was obtained at 6 (12 times), 6′ (5 times), and 81; whereas flexion alone was obtained at

$$\}, \left\{\begin{matrix}82\\85\end{matrix}\right\}, 87.$$

At centres 11, 79, and 80, viz., the neutral ground between the two extremes just detailed, both flexion and extension were nearly equally represented, with, however slight predominance of the former.

(b.) *Primary*—Of the 50 total or absolute movements of the elbow, only 9 were primary, this notably illustrating its subordinate importance. Of these, 6 were extension and 3 were flexion. The distribution of these primary movements was the same as that of the absolute movements.

REPRESENTATION OF THE MOVEMENTS OF THE SHOULDER. (See Plate 42, fig. 20.)

(i) *Total or Absolute Representation.*—Altogether 62 movements of the joint were observed, occurring at the following centres, in order of diminishing frequency :—

$$, 82, \left\{\begin{matrix}80\\83\end{matrix}\right\}.$$

The important fact here exhibited, namely, that the shoulder is not represented at centres 85 and 87, will not escape notice (*vide* March, *infra*). On the other hand, of 14 total primary movements at centre 79, the shoulder claims no less than 13; and for centre 11, out of a total of 14, it claims 12. Thus, the localisation of the shoulder, like that of the thumb, is very perfectly defined.

(ii.) *Primary Representation*—The shoulder, like the thumb, being an important joint in the initiation of movements, moved primarily 34 times at the following centres, in the order of diminishing intensity :—

$$79, 11, 81, 6, \left\{\begin{matrix}80\\82\end{matrix}\right\}.$$

(iii.) *Character of Movement.* (a.) *Absolute.*—Of the total of 62 movements,

28 were adduction,
15 ,, advancing,
11 ,, retraction,
4 ,, elevation,
3 ,, rotation in,
1 was rotation out.

Adduction.—Occurred at :—

$$11,\ 79,\ \left\{\begin{matrix}6\\81\end{matrix}\right\},\ \left\{\begin{matrix}80\\82\\83\end{matrix}\right\},\ 6'.$$

More than half (15) of the instances were observed at 11 and 79. The same thing was observed for the movement of retraction, the explanation probably being that these movements are associated, as we have shown in addition that this is the region of greatest representation of the joint.

Advancing.—This movement—one of great importance and interest—with the exception of being once observed at centre 82, was represented solely in front of the fissure of ROLANDO, namely, at 6 and 6′ (8 times and 6 times respectively).

Elevation was noted 3 times at 79 and once at 11 out of the total of the 4 occasions on which it was observed, thus being closely localised.

(b.) *Primary.*—Of the 36 primary movements of the shoulder (*i.e.*, including combinations),

22 were adduction,
9 ,, retraction,
4 ,, elevation,
2 ,, advancing.

Primary movement of adduction was observed at :—

$$\left\{\begin{matrix}11\\79\end{matrix}\right\}\ \ 6,\ 81,\ \left\{\begin{matrix}6'\\80\\82\end{matrix}\right\}$$

11 and 79 equally gave 7 instances of this movement, so that it was represented 14 times out of 22. Retraction occurs almost entirely at 11 and 79.

It will now be fitting to discuss the order of combination of the movements of the various segments

March or Sequence of Movements in the Segments of the Upper Limb (see Table II and fig. 14).

As the centres in which the upper limb is represented are so few in number in the present research, we have deemed it best to give the march of the movements in full at each spot, in a tabular form.

Centre	Primary.	Secondary.	Tertiary
11	Shoulder add , retract.	Elbow flex	Fingers extend Wrist ext
79	Shoulder, add, retract, elevate	Elbow flex	Fingers ext
80	Border centre .	See p 238	
81	Border centre . .		
82	Wrist pronated	Fingers interosseal flex	Elbow flex Shoulder adduct
83	Thumb flexed, opposed .	Wrist pronated. Fingers flexed.	Elbow flexed Shoulder add (2)
85	Thumb flexed, opposed. Index opposed	Fingers flexed .	Wrist extend Elbow flex.
87	Thumb flexed, opposed	Fingers flexed	Wrist extend, supinate. Elbow flex

The march in this, the posterior half of the ascending parietal convolution, is more differentiated than that of the anterior half and, *a fortiori*, than that of the ascending frontal convolution.

In the upper part of the region it passes steadily down the limb, and in the lower part as steadily up the limb

In this connection it is very important to observe the real position and value of the index finger. Thus, at centre 85 the march is very distinctly in the order of. thumb, index finger, the other fingers, wrist, and elbow. So at this part, where, as we have already seen, the index possesses some primary representation, it forms a distinct item in the march Further, it is most noteworthy that the wrist is invariably pronated in the upper part of the region now under consideration. The importance of this fact has already been alluded to in considering the necessary succession of movements in the performance of the highly evolved actions of the thumb and index finger.

At the same time, it is of great interest, in connection with the development of psychical energy, to see that the representation of the shoulder does not proceed lower than centre 83, while at the same time also the representation of the thumb extends upwards to, but not beyond, the same centre.

Character of Movement in the March.

There are several differences in the character of the successive movements represented in the ascending parietal convolution and those in the ascending frontal convolution. Thus, the shoulder in the parietal gyrus, instead of exhibiting the representation of "advancing," as in the frontal gyrus, is almost invariably adducted and retracted (rarely elevated) at the centres 11 and 79.

PART VII.—MISCELLANEOUS FACTS.

There are several facts of general interest which have come to light in the course of our experiments.

(1) *The Border Centres* (see fig. 3).

We have employed this term to denote those centres which are situated along the lines separating continuous areas of representation.

The centres which come into this category are —

31, 36, 37, 38, 39, 50, 51, 6, 6′, 80.

The representation of function at each of these centres is best seen by summing the absolute representation at each point, and the results of this method we shall now state.

Thus, for example, at centre 31—

Head turned to the opposite side	7	times
Head and eyes turned	3	,,
Eyes opened	5	,,
Eyes turned to opposite side	3	,,
Shoulder advanced.	7	,,
Shoulder rotated	3	,,
Elbow extended	5	,,
Elbow flexed	2	,,
Wrist extended	4	,,

Thus centre 31 is clearly the seat of a simple fusion of the movements of the upper limb and those of the head and eyes. Centre 31 thus serving as an example, it will be similarly found on referring to Table I. that at—

Centre 36	We have fusion of the movements of the	Head and eyes and Upper limb.
„ 37 „ 38 „ 39	„ „ „ „	Head and eyes, Upper limb, Lower limb
„ 50	„ „ „ „	Head and eyes, Upper limb, Lower limb.
„ 51	„ „ „ „	Head and eyes, Upper limb, Lower limb
„ 6 „ 6′ „ 80	„ „ „ „	Upper limb, Lower limb.

From the extreme limitation of the effects of excitation in the thumb region, it is clear that the fusion of representation observed at the above described border centres cannot be due to spread of the current, but is to be interpreted as evidence of the gradual character of the evolution of representation of movements in the cortex. Such evolution would suggest the overlapping of the function of one region by that of another, and the more so in proportion as the parts are commonly moved in association.

(2) *Epilepsy.*

This we observed to follow the weak excitation, we always employed, at centres—

33, 40, 50, 51⁽²⁾, 54⁽²⁾, 58, 62, 65⁽²⁾, 67, 68, 69, 6′, 72, 75.

(2) Noted twice.

It will thus be seen that the focus of the area of representation of the lower limb is the commonest seat of epileptiform disturbance. This may be due to the fact that the different regions of the lower limb area do not equally respond to the same stimulus, so that the same current just sufficient to evoke movement from one centre may cause overaction of another. Though it is undoubtedly a fact that some centres are more easily excited than others, still we do not put this prominently forward in any other sense than as a suggestion towards the interpretation of the above-described localisation of the tendency to the development of epileptiform convulsions.

(3) *Movements of Second and Third Toes.*

In Monkey 40, centre 65, and in Monkey 38, centre 68, the second and third toes began the movement of the limb, independently of the other toes. The movement in the first case was that of extension of the second and third toes, in the other it was that of opposition. Of course, in the Monkey, the second toe is the homologue of the index finger, and consequently is occasionally associated in movement with the hallux, as a primary movement; thus, at centres 65 and 68 in Monkeys 25 and 40 respectively, separation of these two digits was observed in the former, followed by extension of all the toes, while in the latter opposition took place. The march of the movements at these centres makes it quite clear that in these instances the second and third toes occupy undoubtedly a truly primary position, since movement of these is followed by that of all the other toes.

(4) *Purposive Movements.*

(a.) *Head and Eyes.*—It is well worth while to shortly review the so-called voluntary or purposive movements in the light of the facts detailed in the foregoing pages. In the first place, rotation of the head and eyes to one side is a necessary accompaniment of all the highest movements. This will probably explain the fact that this rotation of the head and eyes is represented over the whole breadth of the hemisphere reaching from near to the fissure of SYLVIUS below to the middle line above. It is thus in close apposition, from below upwards, to the areas for the face, the upper, and the lower limbs, respectively. It is, moreover, the area which intervenes between the presumably higher psychical centres of the præfrontal region and the lower areas for the face and limbs; hence, it seems probable that impulses proceeding from these higher centres will traverse the area for the head and eyes on their way to the areas for the limbs

(b.) *Upper Limb.*—We can, with advantage, add to what we said about the movements of the upper limb in our former paper. Some of these movements we have already discussed in considering the mode of the march (p. 237), but to these considerations we would like to add one or two more of a wider nature. It is time to consider whether we cannot elucidate the fundamental principles which underlie the development of the mechanism for the performance of so-called voluntary actions. In the first place, we cannot pass by the obvious fact upon which we think we are now entitled to speak with some degree of certainty, viz., the suggestive difference between the functional activity of the ascending frontal and ascending parietal portions of the upper limb area.

While at the upper part (especially anteriorly) of the ascending frontal portion we find represented, as an initial movement, advancing of the whole limb with extension of all the joints, behind the fissure of ROLANDO the converse exists, and accordingly we find there the function of adduction and retraction of the shoulder with flexion of the elbow.

Summing all these facts together, we would advance the suggestion that an exact parallelism exists between the topographical relations just described and the sequence of movements in such a very frequent purposive action as that of, first, directing the gaze upon an object; next, reaching forward of the upper limb with extension of the joints to seize it, and, thirdly, the withdrawing of the aim with adduction of the shoulder, and carrying of the hand to the mouth by flexion of the elbow.

We are loath to lay too much stress on these deductions, as they are necessarily speculative, and also because we feel that a great deal has yet to be done in explanation of the fact that there are several movements relatively frequently performed by the head and eyes or the limbs, and yet which we have not been able to elicit by electrical stimulation from the regions in which they are presumably represented.

For instance, we have never observed the movement of direct upward rotation of the eyeballs, nor even circumduction of the shoulder, nor, to any marked degree, extension of the hip.

It seems to us probable that the absence of these special movements is owing to the method of analysis. The excitation of the so-called motor cortex by a faradic current is most obviously a very different effect-producing agency to the normal passage of a nerve impulse from the sensory perceptive areas, as occurs in the early stages of an effort of volition. What we mean, in short, is, that we cannot, with the present means at our disposal, apply a minutely localised excitation to one small group of corpuscles, and so cause them to discharge, without at the same time arousing into equal, or perhaps under certain circumstances even greater, activity other contiguous and possibly allied combinations of movements.

(5) *Opening of the Eyes.*

In one Monkey (No 25) we observed in stimulating centres 32 and 33, that the two eyes did not open synchronously, but that the eyelids of the eye on the opposite side to that of the cortex stimulated opened before the eyelids of the same side. The time between the two movements was very slight, but still it shows that, although this movement is usually strictly bilateral, yet in exceptional instances the eyelids of the opposite side tend to act before those of the same side.

Abbreviations

Hd = Head
$\left.\begin{array}{l}\text{Hd.}\\ \text{E.}\end{array}\right\}$ = Simultaneous deviation of Head and Eyes.
L = Left, *i.e.*, opposite side to that stimulated
E = Eyes.
Sh. = Shoulder

Centre	Primary movement			Secondary		Tertiary
14	$\left.\begin{array}{l}\text{Hd}\\ \text{E}\end{array}\right\}$ 13	Hd to L, 3 E to L, 3-5		Eyes open, 4 Hd. to Sh., 1		
15	$\left.\begin{array}{l}\text{Hd}\\ \text{E}\end{array}\right\}$ 9	Hd to L, 5 E to L, 3		Eyes open, 2 Hd to Sh, 3		
16	$\left.\begin{array}{l}\text{Hd.}\\ \text{E}\end{array}\right\}$ 7	Hd to L, 6 Eyes to L, 2 Eyes open, 3		Hd to L, 3 Eyes to L, 4 Eyes open, 1 Hd to Sh, 2		
17	$\left.\begin{array}{l}\text{Hd}\\ \text{E}\end{array}\right\}$ to L, 11	Hd to L, 3 Eyes to L, 3 Eyes open, 1		Hd to L, 3 Eyes to L, 2 Eyes open, 2 Hd. to Sh, 1		Hd to Sh, 3
18	$\left.\begin{array}{l}\text{Hd}\\ \text{E.}\end{array}\right\}$ to L, 7	Eyes to L, 2 Eyes open, 2 Hd to L., 1 Hd to Sh, 1		Hd to L, 2 E to L, 2 Eyes open, 1 Hd to Sh, 2		
19	Hd to L, 5	$\left.\begin{array}{l}\text{Hd}\\ \text{E}\end{array}\right\}$ to L, 3 Eyes open, 2 Eyes up, 1		Eyes to L., 4 Hd to L, 2 Eyes open, 1		Eyes to L, 2
20	Hd. to L., 7	$\left.\begin{array}{l}\text{Hd.}\\ \text{E}\end{array}\right\}$ to L, 3 Eyes open, 3	Eyes to L, 1	Eyes to L, 5 Hd to L, 2 $\left.\begin{array}{l}\text{Hd}\\ \text{E.}\end{array}\right\}$ to L., 2		Hd to Sh, 1
21	Hd to L., 5	Eyes open, 1 Eyes to L., 1		Eyes to L., 2 Hd to L, 1 Eyes open, 1		Eyes to L., 2
22	Hd. to L, 8	$\left.\begin{array}{l}\text{Hd.}\\ \text{E.}\end{array}\right\}$ to L., 5	Eyes to L, 2 Eyes open, 1	Eyes to L, 6 Eyes open, 2		Hd to L, 1 Eyes open, 1
24	Hd to L, 5	Eyes open, 3	$\left.\begin{array}{l}\text{Hd}\\ \text{E}\end{array}\right\}$ to L., 2 Eyes to L., 2	Hd. to L, 2 Eyes to L., 2 Eyes open, 1		Eyes fixed, 1
26	Hd. to L, 2 Eyes open, 2	Eyes to L., 1		Eyes open, 2		
27	Eyes open and turn, 1 (Very slight and slow)					
26′	Hd. to L, 5	Eyes open, 3		Eyes to L, 8		
26*a*	Hd. to L, 6	Eyes open, 4	$\left.\begin{array}{l}\text{Hd}\\ \text{E}\end{array}\right\}$ to L, 1	Eyes open, 3 Eyes to L., 2 Hd. to L., 1		Hd to L. (25°), 1 Eyes open, 1 Eyes straighten, 1
26*b*	Hd. to L., 5	Eyes open, 4		Eyes to L, 2 Eyes open, 2 Hd. turns, 2		Hd. to L, 1
26*c*	Hd to L, 2 Eyes to L., 2	Eyes open, 2				
26*d*	Hd. to L, 1 Eyes to L., 1					
28	Hd. to L., 7	Eyes open, 5	$\left.\begin{array}{l}\text{Hd.}\\ \text{E.}\end{array}\right\}$ to L, 2 Eyes to L., 1	Hd. to L., 2	Eyes to L, 1 Eyes open, 1	

Quaternary	Nil	Total	Remarks.	Centre
	0	19		14
	1	19	Weaker than 14 in 7 out of 18, nystagmus to L, 1	15
	1	19	Nystagmus, 1, eyes up and out (secondary), 1, horizontal (secondary), 1	16
Eyes up and out, 1	1	18	Less than 14, three times	17
	3	18		18
	6	17	Two cases more than 18	19
	4	18	Less than 14, 15, or 16, once, less than 14, once, greater than 16, once, eyes fixed, not turn, twice	20
	10	17	In one case included in the "nil" column the left ear retracted	21
	2	18	Eyes down, twice, eyes and head moved to opposite side in jerks	22
	3	15	All movements were slow and slight, and one noticed in jerks	24
	13	18		26
	17	18	The one positive result was probably due to "*w*" extending less posteriorly than usual	27
	6	14		26′
	5	16		26*a*
	7	16		26*b*
	6	11		26*c*
	3	5		26*d*
	8	18		28

Centre.	Primary movement.			Secondary.		Tertiary	
28a	Hd. to L., 6	Eyes open, 4	$\left.\begin{array}{l}\text{Hd.}\\ \text{E}\end{array}\right\}$ to L, 1 Eyes to L, 1	Hd to L., 3	Eyes to L, 2 Eyes open, 1		
28b	Hd. to L, 2 E to L, 2 E open, 2			Hd. to L., 1			
28c	Hd to L, 1 E open, 1 E to L, 1			Hd. to L, 1			
29	Hd. to L, 4	$\left.\begin{array}{l}\text{Hd}\\ \text{E}\end{array}\right\}$ to L., 3	E open, 1 E. to L, 1	E to L, 2	$\left.\begin{array}{l}\text{Hd.}\\ \text{E}\end{array}\right\}$ to L., 1 E. open, 1		
30	Hd to Sh, 1 (?) E open, 1 (?) E to L 1 (?)						
31	Hd to L, 7	$\left.\begin{array}{l}\text{Hd}\\ \text{E.}\end{array}\right\}$ to L, 3 E. open, 3	E to L, 1 Wrist ext., 2 Sh. adv., 1	Hd to L, 3 Elbow ext, 3	E open, 2 E. to L., 2 Sh adv, 2 Elbow flex, 2	Sh adv, 4	
32	Hd. to L, 12	E open, 1 $\left.\begin{array}{l}\text{Hd to L}\\ \text{E open}\end{array}\right\}$ 1	$\left.\begin{array}{l}\text{Hd to L}\\ \text{E to L}\end{array}\right\}$ 1	E. to L, 5 E. open, 6		E to L, 3 E up, 2 $\left.\begin{array}{l}\text{Finger ext.}\\ \text{Wrist ext}\end{array}\right\}$ 1	
33	Hd. to L, 10	E open, 2 $\left.\begin{array}{l}\text{Hd}\\ \text{E}\end{array}\right\}$ to L., 2	$\left.\begin{array}{l}\text{Hd. to L.}\\ \text{E open}\end{array}\right\}$ 1	E. to L, 7	E open, 6	E to L., 2	
34	$\left.\begin{array}{l}\text{Hd}\\ \text{E.}\end{array}\right\}$ to L., 6	E to L, 3 Hd. to L, 4	$\left.\begin{array}{l}\text{Hd to L}\\ \text{E open}\end{array}\right\}$ 2	E open, 4 E to L., 4	Hd. to L, 1	Hd. to L., 2 E to L., 1	
35	Hd. to L., 4	$\left.\begin{array}{l}\text{Hd to L.}\\ \text{E to L}\end{array}\right\}$ 2 E to L., 2	$\left.\begin{array}{l}\text{Hd to L}\\ \text{E open}\end{array}\right\}$ 1 E. open, 1	E to L., 2	$\left.\begin{array}{l}\text{Hd.}\\ \text{E.}\end{array}\right\}$ to L, 1 Hd to L, 1		
36	Hd. to L, 6	Sh. adv., 4 $\left.\begin{array}{l}\text{Hd.}\\ \text{E}\end{array}\right\}$ to L, 3	Wrist ext., 1 Toes ext., 1 E open, 1	Elbow ext., 3	Sh. adv, 2	Elbow ext, 3	Wrist ext.
37	Hd. to L, 5	$\left.\begin{array}{l}\text{Hd.}\\ \text{E}\end{array}\right\}$ to L., 2 Hip, 2 Ankle, 2	Sh adv, 1 E. open, 1	See "Remarks"			
38	Hd to L, 6	Hip rot out, 1 Hip flex., 1 Ankle evert, p'ant. ext, 1					
39	Hd. to L., 7	$\left.\begin{array}{l}\text{Hd. to L.}\\ \text{Eyes open}\end{array}\right\}$ 3	$\left.\begin{array}{l}\text{Hd.}\\ \text{E}\end{array}\right\}$ to L., 2 E. open, 1 Ankle evert., 1	E. to L, 4	Hd to L, 1 E. open, 1		
40	Hd. to L., 7	$\left.\begin{array}{l}\text{Hd. to L.}\\ \text{E open}\end{array}\right\}$ 4	$\left.\begin{array}{l}\text{Hd.}\\ \text{E.}\end{array}\right\}$ to L, 3 E. to L., 1	E to L., 4	E open, 2		
41	Hd. to L., 7	E. to L., 3	$\left.\begin{array}{l}\text{Hd.}\\ \text{E.}\end{array}\right\}$ to L, 2 $\left.\begin{array}{l}\text{Hd. to L.}\\ \text{E. open}\end{array}\right\}$ 2 E. open, 1	Hd. to L., 3 E. to L, 3	E. open, 1 $\left.\begin{array}{l}\text{Hd. to L.}\\ \text{E open}\end{array}\right\}$ 1		

Quaternary	Nil	Total.	Remarks	Centre
	4	16		28*a*
	7	18		28*b*
	6	9		28*c*
	6	15	Slight nystagmus at break of current	29
	11	14	Motor representation here probably very imperfect	30
Sh. rot. out, 3 Wrist ext, 2 Elbow ext, 2	1	18	As a tertiary movement, there occurred once each —Hd. to L., wrist extended; wrist pronated, flexion of fingers. As a quaternary movement, there occurred once each —Hd to L, elbow flexed	31
	1	16	In Monkey 25, L eye opened before R. at each of these centres. In 33 epilepsy noticed. Pupil dilated once	32
	2	17		33
	1	16	Muzzle up twice	34
	4	14	Muzzle up once In two cases 35 < 34	35
	1	17	Fusion of movements of head and eyes with extension movements of upper limb occurred ten times Movements of leg occurred twice	36
	3	16	There was fusion of head and eye movements with those of limbs, thus—with those of arm, 4, with leg, 3, with arm and leg together, 5	37
	5	14	No definite secondary movement, but there occurred twice.—extension of all toes, knee, and hip, and once each —eyes open, eyes to L., shoulder flexed; elbow extended; toes extended. As tertiary movement, once.—shoulder advanced, elbow extended, knee extended, confused. Muzzle raised up, 1	38
	0	14	As secondary movement there occurred once each —shoulder advanced, elbow extended, hip and knee flexed, ankle inverted, toes extended In one case there was observed after the secondary movement —extended hallux, flexed hip and knee, arm advanced, head and eyes to L. In the primary movement of the eyes opening, occurring once, the L. eye opened before the R	39
	2	17	Muzzle raised up in two cases; pupils dilated in two cases, arm advanced late and slight in one case, leg once very late; L. eye open before R., once, epilepsy, once	40
	1	16	Pupil dilated, 1, muzzle raised up, 1, arm and leg affected together, but late, 1	41

TABL

Centre	Primary movement			Secondary		Tertiary	
42	Hd to L, 3 Hd. E. } to L, 3 E to L, 3			E. to L., 3	Hd. to L., 1		
43	Hd to L, 6	Hd. E } to L, 1 Hd. to L. E. open } 1		E to L, 3			
44	Hd to L, 7	Hd to L E open } 4	Hd E } to L, 1	E to L, 7			
45	Hd to L, 5	Hd. to L. E open } 4	Hd. E } to L., 3	E. to L, 5	E. open, 1	E to L, 1	
46	Hd to L, 4	Hd E. } to L, 1	Hd. to L. E open } 1 E. to L., 1	E to L, 4	Hd to L, 1 E. open, 1	E to L, 2	
47	Hd. to L., 3	Hd. E } to L, 1	Hd to L. E open } 1	E. to L, 4	E open, 1 Sh. add., 1	E to L, 1	
48	Hd. to L, 3	E. to L., 1 Hd E. } to L, 1	Hd to L. E. open } 1 E open, 1	E to L, 5	Hd. to L, 2 E. open, 1	E to L., 1	
49	Hd to L, 5	E to L, 1	Hd to L E open } 1	E. to L., 2	Hd. to L., 1		
50	Hd. to L, 3 Upper limb, 5 Lower limb, 3	Hd. to L. Sh. adv. } 1			See "Remarks"		
51	Hip, 3 Hallux Toes } 3	Hd. to L, 2	Ankle dorso-flex., 1	Shoulder advanced, 3	E to L. Hip flex, 1	Leg flexed, 1 Knee confused, 1 Ankle dorso-flex., 1	
52	All toes ext., 6	Knee flex, 1 Hd to L., 1 Hip extend., 1	Sh. adv, 1 Hd. to L E open } 1	Ankle dorso-flex., 3	Sh adv, 2 Hallux extend., 2 Hip rot out, 1 E. open, 1	Hip flexed, 3	Hd to L., 1 E to L, 1
54	All toes extend., 7	Hip flex., 5	Knee flex, 3	Ankle dorso-flex. ,, invert. } 4	Hip flex, 2 Knee flex., 1 Hallux ext, 3 Hallux flex., 1 Small toes flex., 1 L. abdomen, 1 Arm, 1	Arm advanced, 8 Knee flex., 3 ,, ext., 1 Ankle dorso-flex, 1	
55	Small toes extend., 6	Hallux extend., 2 Hallux opposed, 2	Hip rot. out, 2 Hip flex., 1	Knee flex., 4	Ankle dorso-flex, 2 ,, ext. invert., 1 Hip flex., 1 Hip rot. out, 1	Ankle dorso-flex, 2 ,, invert, 1 Knee ext., 2 ,, flex, 1 Hip flex., 1 ,, ext., 1	Hip flex., 1 ,, ext., 1 Toes ext., 1 Hallux flex., 1

I (continued).

Quaternary	Nil	Total	Remarks	Centre
	6	15	Muzzle raised up, 2, Hd. to shoulder, 1, pupils dilated, 1	42
	6	14	Movements of head were associated with those of the arm and leg together, three times, with the arm only in two cases	43
	4	16	Muzzle raised up, 2 In one case there was —ext hallux, eversion ankle, flex hip and knee In another, L hip was flexed and adducted	44
	4	16	Muzzle raised up twice	45
	5	12	Muzzle turned down at end of movement of turning head, 1 Hd. drawn to shoulder, once	46
	2	12	The upper limb was affected twice, and the lower limb, once. Muzzle raised up, 1	47
	3	15	Muzzle raised up, 3; arm and leg combined were affected, 1, Hd drawn down to shoulder, 1	48
	5	12		49
	2	14	Epilepsy occurred once This number being the border-land of the centres for movements of the head, the upper and lower limbs, it was impossible to find any definite march of movements, owing to the different results obtained	50
	1	10	Epilepsy occurred twice. The primary movements of the hip were extension, flexion, and abduction	51
	2	13		52
	1	14	Epilepsy twice in lower limb, not in the upper	54
Arm. adv., 5	3	14		55

TABLE

Centre.	Primary movement.	Secondary	Tertiary
58	All toes ext., 6 Hallux flex., 1 „ ext., 1 Ankle invert. Ankle dorso-flex. } 2 Sh. adv. slight, 1	Ankle dorso-flex., 2 Ankle ext, 1 All toes flex., 2 Hip Knee } flex, 2 Hip abd, 1	Hip, 3 Knee, 2 Ankle, 2 Toes, 1
59	All toes ext, 4 Hallux flex., 1 „ ext, 2 „ add., 1 } 4 Ankle evert, 1 Ankle dorso-flex, 1 Ankle invert, 1 } 3 Hip and knee flex, 1	Ankle, 6 Small toes, 4 Hallux add., 2	Toes (small), 2 Hip flex., rot. out, 6 Knee, 3 Sh, 1
61	Hallux ext, 4 Hallux add. and opp, 3 } 7 All toes ext., 5 „ „ flex, 1 } 6 Ankle evert., 2 Ankle dorso-flex., 1 } 3 Hip ext, 1	Ankle invert, 7 Ankle dorso-flex., 2 Ankle plant. flex., 2 Small toes ext., 2 All toes ext, 1 Hallux add, 1 Hip rot out. flex., 1	Knee flex, 3 „ ext, 2 Hip flex, 3 „ rot out, 2 „ ext., 1 Sh. adv, 2 Toes ext, 1
6	Hip extend, 4 Sh. add, 3 „ retract., 1 „ adv, 1 } 5 Ankle evert, 1 Hallux ext, 2 Small toes ext, 1 Elbow ext, 2 Wrist pron, 1	Elb ext., 5 Sh flex, 1 Knee ext., 2 All toes flex, 2 „ „ ext., 2 } Hallux ext., 2	Ankle plant. ext., 4 Ankle dorso-flex., 2 } 6 Hip ext., 3 „ rot out, 1 } 4 Knee ext., 1 Sh. rot. in, 1 „ adv, 2 } 3 Wrist ext., 1
6′	Small toes ext., 2 Hallux ext., 1 abd., 1 opp, 1 } 3 Elbow ext., 1 Wrist pronat, 1 Hip rot out flex. } 1 Hip ext., 1 Sh. add, 1 „ adv., 1 } 2	Hallux ext, 1 All toes ext., 2 Ankle dorso-flex., 1 Knee flex., 1 „ conf., 1 } 2 Hip rot in, 1 Sh adv, 1 „ rot in, 1 „ add., 1 } 3 Elb ext., 2 „ conf., 1 } 3 Fingers flex, 1	Small toes flex, 1 Ankle dorso-flex, 2 Knee ext, 1 Hip ext., 2 Sh. adv, 2 Wrist pron., 1
62	Hallux ext., 5 „ flex., 3 } 8 Small toes ext., 3 Small toes flex, 2 } 5 Ankle evert., 3 Ankle plant. ext., 1 Ankle dorso-flex., 1 } 5	Small toes ext., 4 „ „ flex, 1 „ „ conf, 1 Ankle invert, 2 Ankle dorso-flex., 1 } Hip flex, 2 „ ext, 1 } Hallux ext., 1 „ add, 1 }	Hip, 3 Ankle, 3 Toes, 4 Knee, 3
64	Small toes ext., 5 All toes ext. and sep., 4 All toes flex, 1 } Hip ext., 1 „ flex, 1 } Ankle evert., 2 Arm adv, 1	Hallux ext., 3 „ conf, 1 „ flex., 2 } 6 Ankle dorso-flex, 2 Ankle evert, 1 } 3 Small toes ext, 1 „ „ flex., 1 } 2 Arm adv, 1 „ add., 1 } 2	Knee flex, 4 Hip flex, 2 „ rot out, 1 } 3 Ankle invert., 1 „ evert., 1 } 2 Hallux ext., 1
65	All toes ext., 3 „ „ flex., 1 } 4 Small toes ext., 4 Hallux ext., 3 „ flex., 2 } 5 Hip rot. out, 2	Ankle dorso-flex, 3 Ankle plant ext., 1 Ankle evert, 1 „ invert., 1 } 6 Small toes ext., 4 Small toes flex, 2 } 6 All toes ext., 2 Hallux ext., 2 „ flex., 1 } 3 Knee flex., 2	Ankle invert., 4 Ankle dorso-flex., 1 } 5 Hip flex., 2 „ rot. out, 2 } 4 All toes ext, 2 Sh. 2
67	All toes ext., 4 „ „ flex., 2 } 6 Hallux flex., 2 „ ext., 2 „ opp., 3 } 7 Small toes ext., 2 Small toes flex., 2 } 4	Ankle dorso-flex., 4 Ankle plant. ext., 1 Ankle evert., 2 „ invert., 1 } 8 All toes ext., 3 Small toes ext., 1 Small toes flex., 1 } 2 Hip conf., 1 „ rot. out, 1 } 2	Hip flex, 2 „ rot. out., 3 } 5 Knee flex, 3 Small toes flex., 1 Small toes ext, 1 } 2 Ankle dorso-flex, 2 Ankle plant. flex., 1 Ankle invert., 1 }

I (continued).

Quaternary	Nil	Total	Remarks	Centre
Hip rot out, 1 Knee flex, 1 Arm, 1	1	12	Epilepsy once	58
Sh adv, 3 All toes ext 2 Ankle invert., 2	1	12		59
Sh adv, 3 Hip flex, 2 Hip abd, 1 Elbow ext. and conf., 2 Knee, 1	0	16		61
Elbow ext, 5 Sh. adv, 4 Wrist ext, 1 Fingers flex, 3 Toes ext, 3 Knee and hip flex., 3 Hip ext 2 Pelvis rot to L, 2 Knee conf., 1 „ ext, 1	1	18		6
Small toes ext., 1 Knee and hip flex, 2 Pelvis rot, 1 Sh. adv, 2 Elbow ext, 2 Fingers flex, 1	1	12	Epilepsy occurs once	6'
Toes, 2 Knee, 3 Ankle, 1 Hip, 2 Arm, 4	0	13	Epilepsy occurred once It is to be noted that, among the small toes, those which were most represented were the 2nd and 3rd, and the 2nd more than the 3rd. In two cases the hallux and 5th toe were associated as a primary movement, but the 4th toe never	62
Arm adv, 3 Hip and knee flex, 3 Toes flex., 2	1	14		64
Hip and knee flex., 6 Knee flex, 3 Ankle, 2 Arm, 2	0	16	Epilepsy occurred twice Note 2nd and 3rd toes	65
Knee, 7 } conf. and flex Hip, 6 } Sh., 4	1	17	Epilepsy once	67

TABLE

Centre	Primary movement.	Secondary	Tertiary.
68	Hallux flex, 5 „ ext, 5 } 10 All toes ext., 3 „ „ flex, 1 } 4 Ankle plant. ext, 3 Ankle dorso-flex, 1 } 4	All toes ext, 4 „ „ flex, 1 „ „ conf., 1 } 6 Small toes ext., 3 Small toes conf, 1 Small toes flex, 1 } 5 Ankle dorso-flex, 2 Ankle evert., 1 Ankle plant ext, 1 } 4 Hip rot. out, 2 Hallux flex, 1 „ ext, 1 } 2 2nd toe opp, 1	Ankle dorso-flex, 3 Ankle plant. ext, 1 Ankle conf, 1 „ invert, 2 „ evert., 1 } 8 Small toes flex., 2 Knee ext., 1 „ flex, 1 } All toes flex, 1 „ „ ext., 1 }
69	Hallux flex., 6 „ ext, 3 Hallux and 2nd toe ext, 2 } 11 All toes ext, 1 Small toes ext, 1 Ankle evert, 1 Ankle plant. ext., 1 } 2	All toes ext, 2 „ „ flex., 2 } 4 Small toes ext, 3 Small toes flex, 1 } 4 Ankle dorso-flex, 2 Ankle plant. ext., 1 } 3 Hallux ext., 1	Small toes ext., 2 Small toes conf, 1 } 3 All toes ext, 1 „ „ flex., 1 } 2 Hip and knee ext, 1 Hip and knee flex, 1 } 2 Ankle plant. ext, 1 Ankle dorso-flex, 1 } 2
70	Hallux flex, 7 „ abd., 1 } 8 Small toes ext, 2 Knee flex., 2 „ rot. in, 1 } 3 Ankle evert, 1 Ankle dorso-flex, 1 Ankle plant. ext., 1 } 3 All toes ext, 1 „ „ flex, 1 } 2	Small toes ext., 4 All toes ext, 2 Hallux ext, 2 Ankle dorso-flex, 1 Ankle plant. ext, 1 Ankle evert, 1 } 3 Hip flex., 1	Ankle dorso-flex., 5 „ confusion, 1 } 6 All toes ext, 1 Sh rot out, 1
71	Hallux flex., 6 „ ext., 5 } 11 All toes ext, 4 „ „ flex, 1 } 5 Ankle dorso-flex., 1 Ankle plant. flex., 1 } 2	All toes ext, 9 Hallux ext., 4 Ankle dorso-flex, 3 Ankle evert, 1 „ invert., 1 } 5 Hip flex, 3 Knee flex, 2	Hip and knee flex., 5 Ankle dorso-flex, 4 „ conf, 1 } 5
72	All toes ext., 5 Small toes ext, 5 Hallux flex, 3 „ ext., 2 } 5 Ankle plant. ext., 1 Ankle dorso-flex., 2 } 3	Ankle dorso-flex, 3 Ankle plant. ext., 1 } 4 Hallux ext, 2 Knee and hip flex., 1	Ankle dorso-flex, 5 „ invert, 1 } 6 Knee and hip flexed, 4
73	All toes ext., 7 Small toes ext, 3 Ankle dorso-flex., 2 Hallux ext., 1 „ flex., 1 } 2	Ankle dorso-flex., 6 Hallux ext, 2 Small toes ext, 2 Hip and knee flexed, 8	Knee and hip flexed, 3 Ankle evert, 1 „ dorso-flex., 1
74	All toes ext., 8 Small toes ext., 1 Ankle dorso-flex, 1	Ankle Knee Hip } flex, 1	
75	Hallux flex, 2 „ ext., 2 } 4 Hip ext., 2 Sh. add., 2 Knee and hip flex., 1 Ankle evert., 1	All toes ext., 3 „ „ flex., 1 } 4 Small toes ext, 1 Knee ext, 1 Ankle evert, 1 Ankle dorso-flex., 2 } 3 Knee and hip flex., 1	Knee and hip flex, 1 Arm add. adv, 1
76	All toes ext., 2 Hallux ext., 1 „ flex., 1 } 2 Hip flex., 2 Small toes ext., 1 Knee flex., 1 Ankle dorso-flex, 1	Ankle dorso-flex, 3 Ankle invert, 1 } 4 All toes ext, 1 „ „ flex, 1 } 2 Hallux ext, 1 Hip flex, 1	Ankle evert., 2 „ conf, 1 Ankle plant ext, 1 Ankle dorso-flex, 1 } 5 Hip rot. out, 1
77	All toes ext., 5 Small toes ext., 1 Hallux ext., 1 Ankle dorso-flex., 1	Hallux ext, 3 All toes ext., 2 Ankle dorso flex, 2 Hip flex., 1	Ankle dorso-flex, 2 „ evert., 1 } 3 Knee and hip flex, 1

I (continued).

Quaternary	Nil.	Total	Remarks	Centre
Hip rot. out, 5 Hip and knee flex, 4 Ankle, 3 Knee flex, 3 „ conf, 2 } 5	0	16	Epilepsy occurred twice The 2nd and 3rd toes, in Monkey 38, opposed towards hallux as a primary movement	68
Hip and knee flex, 5 Ankle dorso-flex, 3 Knee at 90°, 1 Toes confused, 1	0	15	Epilepsy once	69
Hip and knee flex, 5 Knee confused, 1 Hip abd., 1 „ rot out, 2 } 3 Arm adv, 2	0	18		70
Knee and hip flex, 3 Arm abd., 2	1	18		71
Hip flex, 1 „ ext, 1 } 2 Toes sep, 1	1	18	Epilepsy once	72
Hip rot. out, 1 „ flex., 1 } 2 Knee flex, 1 „ rot in, 1 } 2	4	18		73
	8	14		74
	5	17	Epilepsy once	75
Hip and knee flex., 3 Toes sep., 2 All toes flex., 1 Ankle evert., 1	9	17		76
Hip and knee flex., 3 Knee flex., 1 Sh. adv, 1	9	17		77

TABLE

Centre	Primary movement			Secondary			Tertiary	
78	Small toes ext., 4			Ankle dorso-flex., 2 Hallux ext., 1			Ankle dorso-flex., 1	
11	Sh. add., 7 „ retract, 4 „ elevated, 1 } 12	Wrist pronated, 1 Elbow ext., 1		Elbow flex., 5	Sh. add., 1 „ retract, 1 „ rot. in, 1 } 3	Elbow ext., 1	Fingers ext., 4 Wrist ext., 2	Sh. rot. out, 1 Hip ext., 1
79	Sh. add., 7 „ retract, 3 „ elevation, 3 } 13	Wrist pronated, 1		Elbow flex., 5	Fingers ext., 3 Elbow ext., 2		Wrist ext., 1 Hip ext. rot. in, 1	
80	Wrist pronated, 2	Elbow ext., 1 „ flex., 1	Sh. add., 1 Small toes ext., 1	Fingers inteross. ext., 2	Ankle dorso-flex., 1 Sh. add., 1		Wrist ext., 1 Fingers ext., 1	
81	Wrist pronated, 2 Sh. add., 2	Elbow ext., 1 Fingers ext., 1		Sh. retract., 1 Elbow ext., 1	Thumb and fingers flex., 1		Sh. add., 1 Elb. ext. conf., 1 Wrist ext., 1 Fingers flex., 1	
82	Wrist pronated, 2	Sh. add. retract., 1 Elbow flex., 1 Fingers flex., 1 „ ext., 1 } 2		Wrist pronated, 2 Fingers inteross. ext., 2			Wrist ext., 1 Elbow flex., 1 Fingers ext., 1	
83	Thumb flex., 5 „ opp., 2 } 7	Wrist pronated, 4 Fingers flex., 2 „ ext., 1 }	Elbow flex., 1	Fingers flex., 3 „ ext., 1 Index opp., 1 } 5	Wrist ext., 2 Wrist ulnar add., 1 } 3 Sh. add., 1		Elbow flex., 3	Wrist ext., 1 Fingers ext., 1 Sh. add., 1
85	Thumb flex., 10 „ opp., 4 } 14	Index opp., 4	Wrist pronated, 2 Fingers flex., 1	Fingers flex., 8	Index flex., 2 Thumb opposed, 2 Index opposed, 2 Fingers and thumb, 1 Wrist supin., 1		Fingers flex., 2 „ ext., 1 } 3 Wrist ext., 1 „ pron., 1 „ supin., 1 } 3	
87	Thumb flex., 10 „ opp., 6 } 16			Fingers flex., 8	Wrist supin., 1		Wrist ext., 2 „ pronat., 1	Elbow flex., 1

I (continued).

Quaternary	Nil	Total	Remarks	Centre
Knee and hip flex., 1	7	11		78
Elbow ext., 1	1	12		11
	4	14		79
	12	16		80
	6	11		81
Sh. adv, 1 „ add., 1 } 2 Elbow flex, 1 All fingers ext., 1	8	15		82
Elbow flex, 1	3	17	Index finger opposed towards thumb, once as a secondary movement	83
Elbow flex., 3 Fingers flex, 1 Wrist ext., 1	3	19	Index finger opposed four times as a primary movement. Index finger flexed twice and opposed twice as a secondary movement	85
Wrist supin, 1 Elbow flex., 1	2	16		87

DESCRIPTION OF PLATES 40–42.

PLATE 40.

The figs 4 to 13 and 16 to 20 are stippled to show the representation of the absolute movements and the primary movements of the different joints In all of these the intensity of the stippling denotes the degree of representation of the movements of the joint.

Fig. 4 shows the area of absolute representation of turning the head to the opposite side The points of greatest intensity are seen to be just above the horizontal limb of the præcentral sulcus, and the part next to the longitudinal fissure The area is seen to be very extensive

Fig. 4A gives the representation of the primary movement of rotation of the head to the opposite side. When compared with fig 4 it is seen that the point of greatest intensity here is also just above the horizontal limb of the præcentral sulcus, and also next to the longitudinal fissure In the corner formed by the two limbs of the præcentral sulcus the representation is faint, as this is the place where the simultaneous movement of the head and eyes is most marked.

Fig. 5 shows the representation of the primary movement of the simultaneous action of turning the head and eyes to the opposite side. The point of greatest intensity is in the angle formed by the two limbs of the præcentral sulcus, and is in counter-distinction to fig 4*a*, where this part has only a feeble representation of the primary movements for rotation of the head.

Fig. 6. Here the absolute representation of the movements of the hallux are given The greatest intensity is seen to be in front of the upper end of the fissure of ROLANDO, and to a less degree behind this end of the fissure; from these points the representation extends over the whole of the lower limb area, but in a very feeble degree.

Fig. 6A. The representation of the primary movement of the hallux is here seen to be localised almost entirely to each side of the upper end of the Rolandic fissure, and to have its seat of greatest intensity immediately in front of the fissure. The localisation is very sharply defined, and is more exact than any other joint of the lower limb. (*Cf.* figs. 7, 8, 9, and 10)

Fig. 7 gives the absolute representation of all the toes acting together; the representation extends over the whole area for the lower limb, and has its greatest intensity just in front of and behind the most intense representation of the hallux.

PLATE 41

Fig 8. The representation of the movement of flexion of all the toes is here given, and it is seen to be almost entirely in front of the fissure of ROLANDO.

Fig 9 gives the absolute representation of the movements of the small toes; the greatest intensity is seen to be in front of the fissure of ROLANDO, but in front of and below the part occupied by the hallux.

Fig 10 shows the primary representation of the movements of the small toes, and, when compared with fig. 6A, it is seen to occupy that part of the area of the lower limb, which is not occupied by the representation of the primary movement of the hallux, *i e.*, immediately in front of and behind the upper end of the fissure of ROLANDO.

Fig 11 shows the absolute representation of the movements of the ankle It is well marked over the whole of the lower limb area, and is better represented than the next joint, the knee (*cf* fig 12). Its greatest intensity is above the hinder end of the sulcus *x*, and in front of the area for the hallux.

Fig. 12 is the absolute representation of the movements of the knee, it has no special characters, but is fairly evenly distributed over the whole of the lower limb area, in conformity with the secondary character of the movements of this joint.

Fig. 13 The absolute representation of the movements of the hip is here given. While it extends over the whole lower limb area, it is most marked in front of the fissure of ROLANDO, and especially in the more anterior part; its greatest intensity here is further forward than the representation of the ankle (*cf.* fig 11), and it is only slightly represented just in front of the fissure of ROLANDO, the area for the hallux.

PLATE 42.

Fig. 16 gives the absolute representation of the movements of the thumb as observed in the present research. It is seen in a very striking manner to be limited to the lower end of the intra-parietal sulcus and over a small area; its lower edge is sharply defined and its upper border exhibits only a very slight amount of shading off into the contiguous centres. It is the most highly defined of all the segments of the limb.

Fig. 17 shows the absolute representation of the movements of the fingers; it extends more or less over the whole upper limb area (examined in this present paper), and it is more extensive than the representation of the movements of the thumb (*cf.* fig. 16). But while it is only slightly represented in the upper part of the upper limb area, it is very marked at its lower part, and it will be noted that its point of greatest intensity is just above that of the representation of the thumb.

Fig 18. The absolute representation of the movements of the wrist is here seen to extend over the whole upper limb area (here examined), and to be feebly represented at the upper part of this area, but to have its greatest intensity about the middle and just above the point of greatest representation of the fingers (*cf.* fig. 17).

Fig 19 gives the absolute representation of the movements of the elbow. Though it is represented over the whole upper limb area (examined in this paper), it is very slightly marked in the part opposite the lower end of the intra-parietal sulcus, its chief seat being at the upper end of the upper limb area, on a level with the sulcus *x*, and its point of greatest intensity is at this level, immediately in front of the fissure of ROLANDO, and, to a less degree, in the contiguous part behind this fissure.

Fig. 20. Here the absolute representation of the movements of the shoulder is seen to be localised almost entirely to the upper limit of the upper limb area It is most important to observe that the shoulder, alone of all the joints of the upper limb, is not represented at all in the lower part of this area, opposite the lower end of the intra-parietal sulcus—the seat of representation of the movements of the thumb and the fingers (*cf.* figs. 16, 17) The point of greatest intensity is seen to be in front of and behind the fissure of ROLANDO at the horizontal level of the sulcus *x*, the upper limit of the upper limb area.

On comparing figs. 16–20, it will be seen that the most intense representation of the movements of the segments of the upper limbs is arranged in a most perfect gradation from below upwards. The representation of the thumb occupies the lowest part of the upper limb area, *i.e.*, opposite the lowest point of the intra-parietal sulcus; the fingers have their seat of greatest intensity immediately above that of the thumb; the representation of the wrist is situated just above that for the fingers; while the elbow is represented higher up than the wrist, near the upper limit of the area. The representation of the shoulder forms the upper limit of the upper limb area, being localised rather higher up than that for the elbow.

It will also be noted as most important that, whereas the representation of the thumb is confined entirely to the lowest part of the upper limb area, the shoulder is represented almost entirely at the uppermost limit of this area, *i.e.*, the two extreme segments of the upper limb are limited in their representations to the extreme ends of the area.

X. *The Early Stages in the Development of* Antedon rosacea.

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[PLATES 43–47.]

DURING the winter of 1886–87, while occupying the Cambridge table in the Zoological Station at Naples, I obtained an abundant supply of larvæ of *Antedon rosacea* in all the early stages of development.

As I have had no opportunity of examining larvæ from any other locality, the following description must be understood to refer solely to the Neapolitan form; for, though this and the British form are included under the common name of *A. rosacea*, it is possible that the discrepancies between WYVILLE THOMSON's account of the larva (21)* and the one here given may indicate the existence of specific differences which have hitherto escaped notice.

Two stages of larval development are very clearly marked off from one another, (1) the free-swimming larva; (2) the fixed larva, usually known as the pentacrinoid. PERRIER, however (19, p. 118) subdivides this second stage into (*a*) the "cystid," or stalked form without arms; (*b*) the "phytocrinoid," still stalked, but provided with arms and cirri.

This convenient nomenclature is adopted in this paper, in which the development is only traced to the end of the cystid stage; but the term pentacrinoid, instead of being dropped as PERRIER suggests, may, I think, conveniently be retained to denote any stalked larva, whether cystid or phytocrinoid.

The orientation of the larva presents some difficulties. WYVILLE THOMSON assumed that the oral end of the pentacrinoid was the anterior end, and that the stalk was posterior, and in this he has been generally followed. But recently BARROIS (4) has put forward the hypothesis that the stalk really represents the præoral lobe, and that this larva, like many others, fixes itself by its anterior end.

Being persuaded that BARROIS's view is by far the more probable, I have adopted it in this paper, in spite of the confusion which it is likely to cause in comparing my account with those of previous writers. But, since the proper discussion of this question is impossible before the facts of development are known, I must defer such discussion to the end of the paper.

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* The numbers in parentheses refer to the entries in the Literature List at pp 296, 297.

Preservation.—Only the early stages of development gave any trouble, and for these a mixture of corrosive sublimate (two parts) and acetic acid (one part), as recommended by Bateson for *Balanoglossus*, gave the most satisfactory results. Several other preservatives gave excellent anatomical results; but, owing to the presence in the larva of large quantities of food-yolk, I was unable after them to obtain any satisfactory staining which would exhibit the histology.

Of the copulation described by Jickeli (12) I could obtain no decisive evidence, though I was on more than one occasion led to suspect its occurrence. I am, however, certain that it is not usually nearly so complete as he describes, and that it need not last more than a few hours; moreover, the falling off of the pinnules of the female after the extrusion of the eggs is certainly not a normal occurrence, and, as far as my experience goes, never occurs while the animals are supplied with plenty of well-aërated water. Indeed, the position of the eggs—namely, on that side of the pinnule which is turned towards the apex of the arm—would lead us to the same conclusion; for it is evident that this position affords them great protection so long as the pinnule remains attached. Some peculiarities with regard to the times of laying may be mentioned here Often several weeks would elapse without a single fertilised ovum being obtained, and then suddenly several adults would be brought in on the same day, each with a number of eggs on almost every pinnule; and, what was more remarkable, every embryo, not merely on the same parent, but on all the adults brought in on the same day, would be in the same stage of development This enabled me not only to preserve hundreds of embryos at the same time, with the certainty that all were of the same age, but also to predict with accuracy the age of any larvæ which were brought in in the course of the next three or four days. Until late in April, when laying became infrequent and irregular, I met with only a single exception to this rule, that exception being, so far as I could learn, due to the specimens having been brought from two separate localities, instead of, as usual, from one.

The Ovum.—The eggs are always laid, till late in the season, in the morning, probably not much before 8 A.M., and are attached in masses to the pinnules by a sticky secretion, which makes it extremely difficult to detach them without injury Each ovum is about 0·3 mm. in diameter and of a pink colour, and each is enclosed in a transparent and close-fitting vitelline membrane. The embryo usually remains enclosed in its membrane and attached to the pinnule of the parent till the sixth or seventh day, though in this respect they are subject to considerable variations.

In consequence of the extreme opacity of the ovum and the difficulty of staining the nucleus in the presence of the food-yolk, I made no observations on the fertilisation of the ovum.

Segmentation.—The first cleavage furrow usually makes its appearance soon after mid-day, probably at least three hours after fertilisation, and divides the ovum into two equal parts. Segmentation then proceeds in a perfectly regular manner, the segments being equal in size, and the divisions occurring at intervals of about an hour. Very soon the segments begin to range themselves round a central cavity, but the blastosphere is not complete till fully twelve hours after the first cleavage. PERRIER (19, p. 119) describes and figures a blastosphere of about 64 cells, in which four cells are distinctly larger than the rest, and he regards these four cells as indicating the commencement of an invagination , but neither in this stage nor in any subsequent ones do I find such inequalities to be normal, though undoubtedly one can always find at any stage ova in which segmentation has been somewhat unequal. In reality invagination does not take place till a considerably later stage than that figured by PERRIER, and even at the time of its commencement I could detect no inequality in the size of the cells composing the blastosphere. In size and form the cells of the blastosphere do not appreciably differ from those of the epiblast shown in fig. 1 (Plate 43).

The Gastrula.—About twenty hours after fertilisation a depression makes its appearance at one point in the spherical blastosphere, and gradually deepens until a typical gastrula is formed. The blastopore attains its greatest dimensions about the middle of the second day of development ; it then gradually narrows to an elongated slit, which shortens and, finally, about forty hours after fertilisation, closes completely.

The difficulty of rupturing the vitelline membrane without injuring the embryo makes it hard to determine whether the gastrula is ciliated or not : but, as far as I could make out, no cilia are developed till after the closure of the blastopore.

In the early stages of invagination the cells of the hypoblast are considerably smaller than those of the epiblast, owing, apparently, to their more rapid division. This is seen in fig. 1, which represents a section through an embryo about twenty-four hours old. All the cells at this stage are crowded with yolk-spherules, but as yet there is no mesoblast, and the segmentation cavity is filled only with a coagulable fluid.

Very soon after the stage represented in fig. 1 the mesoblast makes its appearance. At first the cells composing it arise only from the apex of the archenteric invagination, but as it increases in quantity more and more of the hypoblast becomes involved in its formation. Whether these mesoblast cells are simply budded off from the hypoblast, or are pushed out bodily from the archenteric epithelium, I was unable to determine.

In the meantime the epiblast cells have greatly diminished in height, though evidently undergoing rapid division ; and, as I could never observe any direct formation of mesoblast from the epiblast, it seems probable that there is a constant invagination going on all this time at the lips of the blastopore, by which fresh hypoblast cells are continually added as fast as the old ones are used up in the formation of the mesoblast ; for the height of the hypoblastic epithelium does not greatly diminish, and the size of the archenteric cavity seldom increases after the mesoblast makes its appearance, and often appears to decrease. The closure of the elongated blastopore appears to proceed from one end only, and leads to considerable changes in the symmetry of the gastrula, as will be evident from fig. 2, and from the diagram, fig 55 (Plate 47), in which the former outline of the blastopore is indicated by dotted lines.

It must, however, be admitted that my sections of this stage are not wholly satisfactory. Fig. 3, in which the blastopore is already closed, certainly represents a normal stage; but it is just possible that the section represented in fig. 2 belongs to an abnormal larva; and in this case fig. 55, in which I have attempted to connect diagrammatically fig 1 with fig. 3, must be given up.

Long before the end of the second day the epiblast cells have attained a minimum height, as seen in fig 2, though perhaps in this figure they are even unusually low, a better idea of their normal height being obtained from fig. 3.

It may be well here to offer a few remarks upon the gastrulæ observed by Gotte (11). In the earliest stage observed, in which a certain amount of mesoderm was already present, he describes four ciliated bands; and in the next stage, corresponding to my fig. 2, he finds also a depression on the ventral side near the pole, which he considers posterior; so that, according to him, almost all the external features which characterise the complete free-swimming larva are already present at this early stage. I have already stated my inability to detect any cilia whatever at this stage. a little later (early on the third day) I find a uniform coating of cilia, but ciliated bands were never visible before the fourth day. With regard to the ventral "Grübchen" figured by Götte, I can only say that I believe it to be accidental. The embryos are so closely packed on the pinnule of the parent that they frequently press against and distort one another. These distortions are not permanent, and at once disappear in an isolated living larva, but they are often preserved in hardened specimens, and I have, among my sections, several instances of such accidental depressions arising in various parts of the body.

Third Day

By the beginning of the third day the blastopore has closed completely. The larva is still spherical or slightly elongated, and in specimens set free from the vitelline membrane it is seen to have a uniform coating of cilia.

The archenteron has a lenticular form, and in longitudinal sections of slightly elongated larvæ is seen to be flattened antero-posteriorly, and to occupy only one-half of the larva, that half being, on the orientation here adopted, posterior (fig. 3). It is of course important to determine the relations of the blastopore to the regions subsequently recognisable in the larva; but the extremely early closure of the blastopore and the absence of any marked external features at this stage make this determination by no means an easy matter. Götte described the blastopore as closing in the middle of the ventral side (11, p 588), but we have already seen that the "Grubchen" which he relied upon as indicating the ventral side was probably accidental. Barrois (3), on the other hand, says that the blastopore closes terminally at the pole which he still calls anterior, but which, in correspondence with his later suggestion, is here called posterior. I cannot pronounce a decided opinion upon this point, though I am strongly of opinion that the point of closure is not terminal, but subterminal, as represented in fig. 2. I am convinced that it is not so near the middle of the ventral line as Gotte represents it, and, indeed, I do not feel sure that it is on the ventral side at all. The analogy of other Echinoderm larvæ would lead us to regard the ventral position as more probable; but if, on the other hand, the line along which the blastopore closes is to be considered as lying between the future mouth and the final point of closure, then it would appear that this final point must be considered *dorsal, for the larval mouth, as will subsequently be shown, appears in the middle of* the ventral side.

It is to be hoped that the investigation of the development of some other species of Crinoid may set this question at rest

Very soon after the closure of the blastopore a transverse constriction appears in the archenteron, and before the end of the day divides its cavity into two approximately equal parts, anterior and posterior, of which the former is, if anything, slightly the larger. Both cavities are flattened antero-posteriorly, and in transverse section the posterior cavity is usually somewhat oval, subsequent changes showing this to be due to a dorso-ventral compression. This stage is represented in fig. 4, in which the elongation of the larva is already well marked.

So far as I am able to make out, no further production of mesoblast takes place from the walls of the posterior vesicle, which is an enterocele pouch, though a certain amount appears still to be formed from the anterior part of the anterior vesicle or mesenteron.

Fourth Day.

By the fourth day the embryo has nearly lost its pink colour, and has become white or faintly yellow. When set free from the vitelline membrane (a process which is sometimes extremely easy, but usually requires some violence) it is found to be somewhat more elongated than on the previous day, and, though still ciliated all over, provided with several transverse bands and a terminal (anterior) tuft of elongated cilia. These ciliated bands will be described in connection with the next stage of development, in which they are much more clearly marked. Besides these we can usually distinguish two slight depressions, marking the ventral side of the larva. The anterior depression has a circular outline, while the posterior one, occupying the middle of the ventral surface, is larger, and is elongated in the direction of the long axis of the body. These depressions were named "pseudoproct" and "pseudostome" by Wyville Thomson; but in this paper the former will be called the "præoral pit," and the latter the "larval mouth." Neither of them can be seen in a larva still confined within the vitelline membrane, and consequently they are rarely seen in sections, but their positions are indicated by two thickenings of the ectoderm, or, more usually, by a single thickening extending over the whole of the anterior pole and running back along the anterior two-thirds of the ventral surface. GOTTE regarded the "larval mouth" as marking the position of closure of the blastopore, but in this, as already mentioned, he was almost certainly wrong.

Figs. 5, 6, and 7 (Plate 43) represent three longitudinal vertical sections through a larva at this stage; fig. 5 being through the left side, fig. 6 median, and fig. 7 through the right side of the same larva.

It will be seen that the enterocele pouch has assumed the form of a dumb-bell, extending from left to right, and that the mesenteron is curving round the constricted part of this dumb-bell towards the posterior end. At the same time two new pouches are growing out from the anterior portion of the mesenteron, though, as yet, they are but faintly indicated; one of them, which is on the left hand side and ventral, is destined to form the hydrocele (fig. 5); while the other, which is the rudiment of an anterior unpaired body-cavity, is median (fig 6)

The posterior enterocele pouch, which, by its constriction, gives rise to the right and left body-cavities, is now bounded by a definite columnar epithelium, but the cells bounding the mesenteron are much lower, and on its anterior side there is some indication of a continued formation of mesoderm. The hydrocele has a somewhat more definite boundary of elongated cells. The structure of the ectoderm is very difficult to make out, but appears to consist of a single layer of narrow, closely-packed cells, which are crowded with yolk-granules and, for the most part, stain deeply; though below the anterior ciliated tuft and along the region of the larval mouth the staining is usually somewhat less intense.

As the day proceeds the separation of the right and left body-cavities becomes more nearly complete, while the two horns of the mesenteron, growing round the constriction which separates these cavities, at length meet and fuse behind it, so as to form a complete ring. At the same time the hydrocele and anterior body cavity become gradually constricted off from the mesenteron, though they remain freely open to one another till the next day.

Figs. 8, 9, and 10 (Plate 43) are taken from a series of approximately transverse sections through a larva three-and-a-half days old, seen from the anterior end. Unfortunately this series was so much overstained that the histology could not be satisfactorily made out, and no attempt, therefore, has been made to represent it.

From these figures the ring-like form of the mesenteron will be easily recognised. Owing to a slight obliquity in the plane of section, the anterior body-cavity appears to turn towards the ventral side, but its real course, though somewhat ventral, is directly forwards, parallel with the thickened ectoderm of the larval mouth.

At a slightly later stage than is here represented the separation of the hydrocele and anterior body-cavity from the mesenteron and of the right and left body-cavities from one another is complete, though the two last remain for a while connected together by a solid cord of cells, which perforates the mesenteron.

The growth of the mesenteron into a complete ring is so peculiar that for a long while I hesitated to regard it as normal; but I have traced it through so many different series of sections, cut in such diverse planes, that I can no longer doubt that it is the usual form of development, though what it may mean and how it may have arisen, I will not venture to suggest.

The description above given of the development of the various cavities differs in some important respects from those of Gotte and Barrois.

Gotte describes the formation of three cœlomic pouches from the archenteron, two lateral and one ventral; the two former being the right and left body-cavities respectively, and the latter being the hydrocele (11 p. 590).

Barrois (3) finds, as I do, that the archenteron first splits into two cavities, anterior and posterior; but in the nomenclature of these two cavities, and the subsequent fate which he assigns to them, his account differs widely from mine. According to him, after the closure of the blastopore follows—"L'étranglement de la vésicule endodermique en deux parties; l'antérieure qui s'allonge pour se partager en vésicule aquifère et intestin, la postérieure qui s'étire en largeur pour se diviser en deux sacs péritonéaux. Ces derniers ne changent pas de place, mais se transforment en deux disques qui se rejoignent en un manchon tout autour de l'intestin."

If we remember that he still uses the old orientation, it will be clear that he describes as a growth of the two peritoneal vesicles round the intestine what I have described as a growth of the mesenteron round the posterior cœlomic pouch, that the hydrocele arises from the former and not from the latter is, I think, sufficiently clear from fig. 8.

Fifth, Sixth, and Seventh Days.

(1.) *External Form.*—By the fifth day the larva has acquired almost all the external features of the completely-developed free-swimming larva of the seventh day; so that the following description applies in all but a few points (to be mentioned later) to any larva from four to six days old.

The general colour of the larva is usually yellowish-brown, but this colour is confined to the non-ciliated portions, so that the ciliated bands and the two ventral depressions (also ciliated), which are all white, are very clearly defined, their degree of distinctness varying with the amount of pigment developed elsewhere. The greatly elongated cilia of the anterior tuft also spring from a non-pigmented area. Besides the yellowish-brown cells the non-ciliated areas also contain a number of the so-called "yellow-cells." By reflected light, if much pigment is developed elsewhere, these cells are very inconspicuous; but when teased out and seen by transmitted light they appear bright green, while the other ectoderm cells, in which but little pigment is present, appear colourless. This green colour renders the name "yellow-cells" a very inappropriate one, but, since they have been so named in a recent controversy as to their nature, to which reference will be made later, I have thought it better to retain this name. WYVILLE THOMSON called them "oil cells"; but, as they do not appear to contain oil, this name is no improvement. It is worthy of note that these cells make their appearance long before the rupture of the vitelline membrane (fig. 13) The ciliated bands are five in number, and their cilia are somewhat shorter than those of the terminal tuft. No trace of cilia was to be found between the ciliated bands. The anterior band is incomplete ventrally, and irregular in its degree of development: usually it becomes lost at each side of the præoral pit (figs. 13 and 15), but sometimes it turns sharply forward, as if endeavouring to complete itself on the anterior side of this depression (fig. 14). On the dorsal side this band runs so close to the extremity of the larva that its cilia frequently show even from the ventral side, producing the impression that the whole anterior end is covered with short cilia (fig. 14).

Each of the other four ciliated bands completely encircles the larva, and the two posterior ones are simply transverse rings; but the two middle bands are only transverse on the dorsal side, being deflected from their course on the ventral side by the larval mouth, which lies between them, and with the ciliated lining of which the third band fuses posteriorly.

The larval mouth varies greatly in size, but is sometimes so deep as almost to cut the larva in two, and is always much deeper anteriorly than posteriorly.

The præoral pit, on the other hand, never attains any great depth, and is often so shallow as scarcely to be recognisable in sections.

The principal difference between the larvæ of the fifth, sixth, and seventh days is one of size, and especially of length. Within the vitelline membrane the larva is always compressed into a spherical, or nearly spherical, form (fig. 13); but when liberated it suddenly elongates to a considerable extent, usually, however, remaining for a time concave ventrally. If set free on the fifth or sixth day it continues to increase in size and to elongate itself, until it usually becomes quite straight (fig. 15); but if not liberated till the seventh day it seldom has time to straighten itself completely before it becomes fixed.

In most broods, but not quite in all, there appeared on the seventh day a circular white spot on the left side, between the third and fourth ciliated bands (fig. 15); as indicated in the figure, it marks the orifice of the "water-pore."

The larvæ examined by me at Naples differed in several respects from those described by WYVILLE THOMSON. The more trifling of these differences are probably due to his method of examining the larva as a transparent object by means of compression, which naturally led to distortion. But the absence of all mention of the anterior ciliated band in his account can hardly be explained thus; and since this band is also omitted in the figures given by BUSCH (5), who obtained his larva in Kirkwall Bay in 1849, it is possible that it is altogether absent in the British form.

That GOTTE did not notice it is less surprising, as he does not appear to have worked much with fresh material, and it is with difficulty recognisable in spirit specimens Of the oral depression described by him as occurring between the fourth and fifth ciliated bands (11, p. 590) I could find no trace.

Although WYVILLE THOMSON asserts that the larva "swims with either extremity in advance indifferently" (21, p 522), I find that in almost all cases the ciliated tuft is directed forwards; indeed, out of hundreds of larvæ examined, I never saw one swim in the opposite direction, except when it encountered an obstacle, in which case it would reverse its motion for a short distance, always, however, resuming before long its original course. The fact that when at rest the cilia all curve towards the anterior end is probably connected with this mode of swimming.

(2.) *Internal Anatomy.*—We left the larva at the end of the fourth day with a ring-like alimentary canal, and four cavities derived from it, namely (1), an anterior body-cavity, running forward into the præoral lobe, and at its posterior end turning slightly to the left to open into (2), the hydrocele, which is at present a simple vesicle; (3 and 4), the right and left body-cavities, which are still connected by a solid cord of cells passing through the mesenteron; but very soon this cord is completely absorbed, so that the mesenteron has no longer the form of a ring, but rather that of a disc flattened between the body-cavities.

Rather before this stage is reached an important change takes place in the positions of the right and left body-cavities. The latter, which lies immediately behind the hydrocele, shifts towards the posterior end, and at the same time towards the ventral surface; while the right body-cavity becomes more and more anterior and dorsal. In consequence of this change, the mesentery separating these two cavities, instead of being longitudinal, assumes an oblique position, which is more easily understood from figures than from a description.

Fig. 21 (Plate 44) represents a horizontal section, seen from the dorsal side, in which the right body-cavity is clearly more anterior than the left; the mesentery is visible on each side of the alimentary canal, and a line joining these two portions of it would represent its course across the back of the larva · in this specimen the mesentery is very decidedly oblique, but in many larvæ on the seventh day it appears, from this point of view, to have an almost completely transverse course. In a lateral view, however, it is always oblique, running from the ventral side backwards towards the dorsal side, as seen in fig. 59 (Plate 47), which is a diagrammatic view of a larva from the right side.

GOTTE (11, p. 591) correctly describes this arrangement of the mesentery, but in accounting for it by a change in position of the body-cavities he has fallen into an error of no little importance, but one which, owing to the different orientation which he employs, is not easy to demonstrate. That which in fig. 21 I have marked "left body-cavity" receives the same name in his account, but then he regards this cavity as occupying the anterior end of the body, and the side marked R in my figure is, according to him, left. I am not here concerned with the question whether his orientation is or is not correct; but I wish to call attention to the fact that if we both used the same orientation we should differ in our nomenclature of the body-cavities; in other words, if we interpret his account in terms of the orientation here adopted, it is the *right*, and not, as I have stated, the *left*, body-cavity which assumes a posterior position.

Besides fig. 21, which has already been explained, figs. 11 and 12 (Plate 43) also support my account. Fig. 11 represents a transverse section, seen from the posterior side, through a larva of the fifth day, passing through the posterior part of the larval mouth, the thickened ectoderm of which marks the ventral side. On the left side is seen the hydrocele, still opening into the anterior body-cavity; while on the right side lies the right body-cavity. The left body-cavity, being posterior to the hydrocele, does not appear in this section; but in fig. 12, representing a section near the posterior end, it is the principal cavity, and lies distinctly more on the ventral side than does the right body-cavity.

Returning now to the general anatomy, we find that the hydrocele and anterior body-cavity are undergoing some important modifications. In fig. 11 they still communicate with one another, but at a slightly later stage I have searched in vain for any such connection. The hydrocele grows towards the right side, and then, curving towards the posterior end, and again towards the left side, it forms a horse-shoe-shaped curve, open towards the left, and lying between the mesenteron and the ventral ectoderm. At first it does not extend much beyond the middle ventral line, but later on it extends very nearly to the extreme right, and forms an almost complete ring, from the ventral surface of which spring the rudiments of five tentacles (fig. 61, Plate 47). After separating from the hydrocele the anterior body-cavity grows towards the ectoderm on the right side, at the level of the blind end of the hydrocele, and finally opens to the exterior between the third and fourth ciliated bands by the "water-pore" already mentioned. The walls of the pore itself are certainly formed by ectoderm cells, but there appears to be no regular invagination of the ectoderm to meet the cœlomic outgrowth. This pore is usually not formed till just before the larva fixes itself. It is clearly the homologue of the "dorsal pore" of other Echinoderm larvæ, but I have avoided this name for it, since in *Antedon* it is distinctly lateral.

So far I have only given a general outline of the changes in the anatomy of the larva between the fifth and seventh days. It will now be well to enter into a more detailed description of a fully-developed free-swimming larva of the seventh day, mentioning such points as have hitherto been purposely omitted, and comparing my results with those of previous observers. The two diagrams (figs. 59 and 60) will be found useful in connection with the following description.

The anterior body-cavity varies considerably in dimensions. It usually forms a conspicuous cavity at the anterior end of the mesenteron, but elsewhere it is quite narrow. Its continuation forwards, where it usually lies close to the ectoderm of the larval mouth, and rather on the left side, is seldom easy to trace for any distance, though that it sometimes has a considerable length is evident from fig. 18 (Plate 44). It is lined throughout, except close to the pore, by an epithelium of much-flattened cells, the pore itself and a small portion of the tube below it being bounded by a cubical epithelium bearing cilia.

The form of the hydrocele has already been sufficiently described. It has a high columnar epithelium with deeply-staining nuclei.

The mesenteron is flattened on the ventral side, where it adjoins the hydrocele, but is convex dorsally (fig 17). It lies far from the larval mouth, and indeed shows no trace of any communication with the exterior; for, as already mentioned, I have been unable to find the ectodermic depression described by GOTTE as the mouth.

The left body-cavity, which fits like a cap over the posterior end of the mesenteron, extends forwards in the median ventral line only as far as the posterior border of the hydrocele (fig 17): it nowhere intervenes between this organ and the ventral ectoderm, but on each side of the former it extends forwards almost to the level of the water-pore. Dorsally, as already mentioned, it does not extend very far forward. Its epithelium, and that of the right body-cavity, is considerably flattened at this stage. While the left body-cavity is for the most part ventral, the right body-cavity is almost wholly dorsal. On the right side, it is true, it nearly reaches the ventral side (fig 59), but on the left it extends no further than the water-pore. It tapers away rapidly as it passes forwards, and at the anterior end of the mesenteron exists only as a small cavity having a semi-lunar form in transverse section, the convexity being towards the dorsal surface. In the centre of the mass of mesoderm which stretches from this point to the extreme anterior end, there runs at this stage a cord of slightly elongated cells No trace of this was present on the fifth day, and even on the seventh day it seldom extends much more than half way from the mesenteron to the anterior pole It usually has a more or less strong ventral curvature, in correspondence with the curvature which, as already mentioned, most larvæ show, until they have been for some time free from the vitelline membrane. In longitudinal sections it is generally possible to trace the right body-cavity forward into this axial cord; and in favourable transverse sections it is even possible to make out that this extension of the body-cavity is divided into five extremely minute cavities, arranged round a central strand (fig. 19). This central strand or *axial organ* runs back to the anterior end of the mesenteron, and it is around it that the right body-cavity assumes the horseshoe-like form above described. Owing to their extremely small size, these five tubular cavities, which clearly form the rudiment of the *chambered organ*, could not be satisfactorily traced back individually into the body-cavity; but, from the fact that two of them appear in horizontal sections (fig. 21), and only one in longitudinal vertical sections (fig. 17), and from certain changes which the right body-cavity undergoes at a later stage, I am led to believe that the diagram (fig. 56, Plate 47) represents their mode of origin; two appear to come off on the right side and three on the left, one of the latter forming in fig. 19 the median ventral chamber. Fig. 56 is orientated for comparison with fig 57 (which will be explained later), and is seen from the posterior end.

Barrois (3) denies altogether the existence of any forward prolongation of the cœlom into this region of the body; but, since it seldom exists till a few hours before fixation, and is much obscured afterwards, this is not very surprising Far more suprising is the fact that the anterior body-cavity and its pore seem also to have escaped his notice.

Gotte, on the other hand, figures an enormously wide prolongation, into which a tapering cord of splanchnic mesoderm runs from the mesenteron He gives no explanation of how this state of affairs arose, and I have no doubt that he has really confused together the anterior body-cavity and the forward prolongation of the right body-cavity.

Perrier, however, accepts Gotte's figure (11, Plate 25, fig. 10) as correct, and attempts to prove from his own sections of the cystid that the chambered organ arises from the fusion along certain lines of a central cord of splanchnic peritoneum with a surrounding sheath of somatic peritoneum (19, pp. 123, 139, and 163). But, as I shall show later, he has overlooked the presence of a longitudinal mesentery, which on his view would be difficult to account for.

The histology of the ectoderm remains to be described. The cells of the ciliated bands are easily recognisable in section, not merely by their arrangement, but also by their small, deeply-stained nuclei, situated for the most part at the inner ends of the cells, and by the marked striation of their outer borders. The nuclei of the non-ciliated cells, on the other hand, are large, stained but slightly, and are situated near the middle of the cell. Among these cells are scattered the "yellow-cells," but these are rarely distinguishable in sections. In fig. 12 they are recognisable by their shrunken and distorted walls, which have a yellow colour after staining with borax carmine; but these peculiarities are probably due to the preservative used (picro-hydrochloric acid), and are by no means always present They sometimes stain deep blue with Grenacher's hæmatoxylin, but the colour is rapidly removed by acid; and, unless decolorisation is checked at precisely the right moment, they are indistinguishable from the surrounding cells. If a living larva be teased out in sea-water, all the ectoderm cells are seen to be filled with refractive yolk-spherules, and the "yellow-cells" differ from the rest only in their colour, which however is not equally developed at all. The yellowish-brown pigment of the other cells appears to be entirely superficial, is not dichroic, and is rarely present in sufficient quantities to be recognisable in individual cells. If a yellow-cell be broken up, we see that the colour is contained in a diffuse form in the yolk-spherules, and innumerable gradations can be found between absolutely colourless spherules and others of a vivid green. The addition of acetic acid at once destroys the colour, clears up the spherules, and brings the nucleus into view, and then the "yellow-cells" are absolutely indistinguishable from ordinary ectoderm cells. Osmic acid also destroys the colour, but does not blacken the contents; so that THOMSON's name of "oil-cells" is without foundation. GOTTE professes to have seen these cells in his sections, and figures them accordingly; but, since in his figures they are made to occur in the larval mouth, from which they are certainly absent in the living animal, I do not feel confident that what he figures were really the yellow-cells at all.

The cells bearing the anterior tuft of cilia differ considerably from those of the ordinary ciliated bands, though they too have a striated border (fig 23). The cells of the præoral pit, however, though generally resembling those of the ciliated tuft, have no striated border. Between the ciliated tuft and the first ciliated band the ectoderm is peculiar in containing a number of long narrow cells, which stain deep purple with GRENACHER's hæmatoxylin, and retain this colour tenaciously in acidulated alcohol. The anterior and deeper half of the larval mouth contains cells which also stain deep purple, but they part with their colour much more readily, and they have strongly striated borders They are seen in longitudinal section in fig. 22 stained with hæmatoxylin, and in transverse section in fig 24 stained with borax carmine, which has but little effect upon them. The posterior half of the larval mouth is lined by narrow, closely-packed cells, which are easily distinguished in sections stained with GRENACHER's hæmatoxylin (fig. 22).

Round the edge of the præoral pit and down the sides of the larval mouth there runs a narrow groove (figs. 22 and 24) which is filled with excessively fine longitudinal fibres. A deep layer of similar fibres, running for the most part from side to side, underlies the whole of the anterior pole (fig 23). they are apparently ectodermic, though where they occur there is seldom any marked line of separation between the ectoderm and mesoderm. From the position and general appearance of these fibres it seems most probable that they are part of a nervous system, and that some at least of the peculiar ectodermic structures connected with them are of a sensory nature.

The Skeleton —The first rudiments of the skeleton make their appearance early on the sixth day, but, owing to the opacity of the larva, they can only be seen in specimens cleared in turpentine and balsam, or partially macerated in potash. In the youngest specimen observed there were already fourteen calcareous nodules, representing five orals, five basals, a dorsocentral, and three stem-joints, but the last-named plates rapidly increase in number. The most anterior plate is the dorsocentral, which lies deeply embedded in the tissues, almost exactly in the centre of the body. From it the stem-joints, which as yet are exceedingly minute, lead back in a longitudinal series towards the anterior end of the mesenteron. The five basals and five orals are of about the same size as the dorsocentral, but much more superficial, lying immediately beneath the ectoderm. Each series of five plates is arranged in the form of a horseshoe, widely open towards the ventral surface, and set obliquely to the long axis of the larva, in fact, each horseshoe may be described as approximately parallel to the mesentery separating the right and left body-cavities, the basals being developed round the former, and the orals round the latter cavity. As a consequence of the fact that they share not only the longitudinal but also the lateral obliquity of this mesentery, the left ventral plate of each series is distinctly nearer the anterior end of the larva than is the right ventral plate of the same series thus the left ventral basal generally lies at about the same level as the dorsocentral, while the right ventral plate of the same series lies at about the level of the posterior stem-joint.

I could discover no indication that the dorsocentral, basals, and orals, were developed in any particular order, though it is probable that all of them are developed before the stem-joints At first all these plates are simple amorphous nodules, but as they increase in size most of them branch out and assume the form of triradiate or quadriradiate spicules, all the rays lying in one plane; and later, by further branching and anastomosis, each forms a flat reticulate plate, lying in the case of the basals and orals parallel with the ectoderm, and in the case of the dorsocentral nearly transverse to the long axis of the body. Fig 47 (*a*), though really representing another plate, will serve to illustrate the form of an oral or basal on the sixth day; while fig. 49 represents one of them on the tenth day.

The stem-joints differ from the dorsocentral and other plates in form. Each is at first a slightly-curved plate, smooth on the concave side (which is directed ventrally), and scalloped on the convex or dorsal side (fig. 47, *b*), but as it increases in size it grows more and more round to the ventral surface, and eventually forms a complete ring (fig. 51), though this does not usually happen till after fixation. At the same time the processes of the convex side grow out more and more, and anastomose with one another.

New stem-joints are constantly being formed at the posterior end, and push the dorsocentral nearer to the anterior end; and consequently the anterior stem-joint is always the oldest and most developed. As is seen in fig. 19, each joint, in its growth into a ring, surrounds the chambered organ.

The number of stem-joints of course varies with the age of the larva, but the process of formation appears to be quite continuous, and no pause at a stage with eight plates, such as is described by GOTTE (11, p. 597), could be observed.

Early on the seventh day some new plates make their appearance at the posterior end of the series of stem-joints; they are three in number (rarely four or five), and in form resemble small basals, though they are developed at a much deeper level than these plates, and are usually nearer the posterior end of the body than the two ventral basals. One of these plates is shown in fig 47 (*a*); and their position with respect to the basals and stem-joints is seen in fig. 45, in which the plates themselves are represented diagrammatically, though their position is carefully copied from actual specimens. These three "underbasals" are at first equal in size, but after a while two of them begin to grow more rapidly than the third, eventually attaining to about double its size.

In order to explain the true positions of these underbasals, we must have a definite nomenclature for the five radii, into which the body of the larva becomes marked out by the appearance of the interradial basals and orals. Fig. 54 is a diagram of the disc of an adult endocyclic Crinoid seen from the oral side, illustrating CARPENTER's system of nomenclature (see 6, p. 89). Taking the anal interradius as a fixed point, he names the radius opposite to it A, and then, passing round the animal in the same direction as the winding of the alimentary canal, he calls the other radii B, C, D, E This nomenclature is adopted in this paper, with this difference, that the radius A is made to depend not on the anus, which is not yet present, but on the water-pore, which, as we shall see, lies in the cystid with the anus in the interradius C D. This pore is shown in figs 45 and 58, and is seen not to be at present directly connected with any one of the skeletal plates.

In fig 58 the animal is supposed to be seen from the posterior end, with the larval mouth directed away from the observer. This orientation is intended to facilitate comparison with the figures of the later stages. We now see that the smallest underbasal lies, not in the dorsal interradius AE, but in the radius A, opposite the interradius of the water-pore.

It is not a little curious how all the plates seem, as it were, to avoid at first the ventral side. This is not so well marked for the orals and basals in fig. 58 as it was at an earlier period, but it is still true of the underbasals and stem-joints; and in the rare cases in which five underbasals were developed they appeared, so far as I could see, to be ranged in the form of a horseshoe, quite as widely open ventrally as that of the basals and of the orals.

FIXATION OF THE LARVA AND TRANSITION TO CYSTID STAGE.

External Form.—As already mentioned, the majority of larvæ are not set free from the vitelline membrane till the seventh day of development. Such larvæ, after swimming actively for about twelve hours, attach themselves to any suitable surface by means of a præoral pit, which then rapidly flattens out into a disc. It is clear, therefore, that the whole ventral side of the larva lies almost parallel with the surface of attachment. For convenience in section cutting, I allowed the larvæ to fix on thin sheets of celloidin; and this method, for which I am indebted to my friend Dr. G. J. VOSMAER, has the advantage that the changes undergone by the ventral surface of the larva subsequent to fixation can easily be followed under the microscope through the transparent celloidin, without disturbing the animal. Fig. 16 is a drawing of a rather unusually large larva made in this way about an hour after fixation. In this figure the ciliated tuft and anterior ciliated band are still present, but these very soon disappear; the four remaining bands, however, not only persist for two or three hours, but usually continue to exhibit a certain amount of motion. A little later all the ciliated bands disappear, and the larval mouth, after first becoming very shallow, gradually narrows and disappears.

At the same time the posterior end gradually rises up, so that the long axis of the larva makes a larger and larger angle with the surface of attachment, and the anterior end, which, though flattened dorso-ventrally, was formerly the widest part of the body (fig. 20), becomes narrow and rounded, so that the whole animal assumes the form of a gradually-tapering club, attached by a flattened disc at its narrow end. Up to this time the larva has remained extremely opaque, but it now rapidly becomes more transparent, and the calcareous plates can be faintly seen even when the larva is viewed as an opaque object.

The larva has now assumed all the characters of the well-known cystid, and the subsequent external changes are correctly figured in THOMSON's paper (21)

This observer's account of the fixation differs slightly from mine. He describes the two ventral depressions, and most of the ciliated bands, as disappearing before fixation; and the larva figured by him as the latest free-swimming form has already the shape of a complete cystid (21, Plate 25, fig. 1). There may, of course, be some difference in this respect between the English and Neapolitan forms; but such larvæ as he has figured did occur frequently, though not normally, among my specimens. They were not, however, as I believe, really unfixed: for in each one that was specially examined some small object, such as a grain of sand, was found imbedded in the tissues at the anterior end (end of stalk); but this object not being sufficient to anchor the larva, the latter had continued to swim about, and had retained its cilia at a later stage than it would otherwise have done. Such larvæ were never observed to undergo any further process of fixation; but, sooner or later, lost their cilia completely, and sank helplessly to the bottom of the tank, where they perished in the débris. Altogether, the larvæ showed a singular want of discrimination in their choice of positions for fixation; besides numbers which thus perished from attaching themselves to objects too small to support them, some attached themselves to the pinnules of the parent, where they never managed to adhere very long; and others to their own cast-off vitelline membranes, which were soon eaten up by bacteria and infusoria.

Another frequent source of destruction of larvæ may be mentioned here. As previously stated, the ease with which the vitelline membrane can be broken is subject to considerable variations. Some whole broods are set free with ease on the fourth day; but in most broods, not only in my tanks, but also in the sea, the majority were not set free till the seventh day, and a considerable number were unable to free themselves even on the ninth or tenth days—long after the majority of larvæ had become fixed. Such prisoners, when at length liberated, were seldom able to fix themselves, and if they did so, usually exhibited considerable abnormalities of form; more often they remained unattached, and either grew into monstrous shapes or remained perfectly spherical. Some of the last-named forms I have liberated as late as the eleventh day; and, though they had lost the two ventral depressions, they still retained some of their cilia in active motion. The internal anatomy of such forms would afford an interesting study, but I have not yet had time to investigate it.

The reason of so much variation in the consistency of the vitelline membrane, leading so often to considerable loss of life, is not easy to see, but it may possibly be connected with the varying conditions to which these animals are exposed. Thus, if the membrane were always of the same strength, a sudden storm might set all the larvæ free at too early a stage of development, and so deprive them of the protection afforded by the pinnules of the parent; while, if the membrane were strong enough to resist such a storm, a continued calm might leave a greater number unable ever to free themselves than at present occur. What value there is in this suggestion must be determined by the examination of other larvæ exposed to the same varying conditions.

Internal Anatomy.—The first changes which occur after fixation are principally histological, and it is not for some hours that the general internal anatomy alters much.

The ectoderm soon loses its distinctness from the mesoderm, the ciliated bands degenerate (fig 20), and histolysis, setting inwards from the ectoderm, rapidly spreads to all the tissues, and results in the obliteration of almost all the previously existing histological differentiation. The details of this process of histolysis are extremely difficult to follow; and both in its mode and degree of action and in the relative times at which it affects different organs it appears to vary considerably. About six hours after fixation the larval mouth has flattened considerably, and presents the very peculiar appearance represented in fig. 26, which should be compared with the section through the same region in a free-swimming larva (fig. 24). The central part, which stains but slightly, no longer shows any cell-outlines, but is traversed by a fine network of threads, and contains a few extremely minute cells, whose nuclei stain intensely, and which may very possibly be phagocytes; while at each side of the groove there lies a deeply-stained mass, containing a few large but inconspicuous nuclei and an enormous number of small deeply-stained nuclei, which apparently belong to cells similar to, but perhaps usually larger than, the phagocytes (?) in the centre. Similar cells have already attacked the ciliated bands in fig. 20.

Some hours later a transverse section through the larval mouth presents the appearance shown in fig. 27. The fine network has disappeared, while the large nuclei have spread towards the centre; the whole mass stains deeply, but no true epithelium appears to be formed. In both this and the previous stage the striated border seen in fig. 24 is still represented by a hyaline region. Besides these details we notice in fig. 27 that two lateral folds are growing across the larval mouth to meet one another in the middle line: they meet and fuse first at the posterior end of the groove, but, their fusion extending rapidly forwards, we find, less than twelve hours after fixation, a completely closed cavity running along the ventral surface, which is shown in longitudinal section as the vestibule in fig. 28. In this figure, and in all subsequent ones of fixed larvæ, the position of the larva has been reversed, and the præoral lobe (stalk) directed towards the observer, since less confusion is likely to arise from this than from altering the orientation of the pentacrinoid larva, with which previous writers have made us familiar.

In the meantime, usually before the invagination of the larval mouth, a number of very minute cells are proliferated into the mesenteron from the centre of the water-vascular ring (fig. 25) these cells soon completely fill the cavity of the mesenteron, where they remain for a considerable time. Since their deeply-stained nuclei are fairly conspicuous, it is surprising that in their figures both GOTTE and PERRIER should have drawn a pale granular mass, which looks much more like a coagulum than a mass of cells. PERRIER, indeed, distinctly states (19, p. 122) that this mass colours almost as completely as the cells of the epithelium of the stomach; he does not, however, represent it so in any of his figures, but generally leaves the stomach empty, while in one place (19, Plate 1, fig. 3) he has drawn, instead, several cells of enormous size—a condition which meets with no support either from his other figures or his description, and one which I cannot but regard as wholly imaginary.

Returning now to fig 28, we see that soon after the invagination of the larval mouth the cavity so formed, which we may call the vestibule, pushes its way rapidly backwards, so that part of it comes to lie opposite the water-vascular ring, while the mass of cells forming its floor envelopes this ring, and fuses with the similar mass occupying the cavity of the mesenteron. Histolysis has by this time invaded the epithelial linings of the various cavities, so as very greatly to obscure their limits.

Hitherto the larva has been lying almost parallel with the surface of attachment; but now, by a rapid growth of the part between the disc of fixation and the vestibule, the long axis of the body becomes more nearly perpendicular to this surface, and at the same time all the internal organs are, as it were, rotated to the posterior, or, as I shall in future call it, the *oral*, pole. By this change the vestibule and the water-vascular ring come to lie transversely to the long-axis of the body (fig. 29), while the body-cavities also undergo some important changes The anterior body-cavity has greatly diminished in size, and it is only in very thin sections that its lumen is at all distinguishable: it is no longer continued into the præoral lobe, but the whole of it has followed the general rotation, and now lies entirely in the inter-radius CD, near the oral pole. The left body-cavity is also much smaller than before, and, having been pushed from the ventral side by the movement of the vestibule, it now lies entirely on the dorsal side, immediately below the mass of cells forming the floor of the vestibule. The position and form of the right body-cavity are but little altered; and, though its five-chambered continuation forwards is no longer visible in sections, it probably still exists, and certainly re-appears a little later (fig. 29). Both right and left body-cavities now grow rapidly round to the ventral surface; but, as the larva has now reached the true cystid stage, further details as to its anatomy may conveniently be postponed.

GÖTTE, as is well known, described the left body-cavity as splitting into two parts, one of which formed the vestibule, while the other remained as body-cavity, and grew round the œsophagus. the latter is the left body-cavity of my account, and the real origin of the former is, I think, sufficiently proved by my figures.

BARROIS (3) has already observed this mode of origin of the vestibule, but he gives no figures, and I cannot discover from his very brief note what his views are as to the origin of the left (or, as we may now call it, the *oral*) body-cavity. PERRIER evidently thinks (19, p 124 note, and p 281) that BARROIS derives this cavity from the vestibule, thus repeating GOTTE's error in a slightly different form; but I cannot feel sure that this is a correct representation of BARROIS's views, since all that he says is that the right and left body-cavities do not change their places, but form "un manchon autour de l'intestin." This does not seem to me to justify PERRIER's statements; but, at the same time, it does not account for the presence of two body-cavities, one oral, and the other aboral, such as we find in the cystid

PERRIER himself believes in the common origin of the vestibule and oral body-cavity; but his figures of this stage show that he has unfortunately only obtained larvæ which had escaped late from the vitelline membrane, and which were consequently somewhat deformed; and in these forms, as I know from experience, the relations of the cavities are excessively difficult to make out, the oral body-cavity in particular being sometimes almost entirely obliterated by the excessive growth of the mass of cells forming the floor of the vestibule. I must, however, protest against the representation of a communication between the vestibule and the oral body-cavity in fig. 11 of PERRIER's memoir: since this communication, if it ever existed, is, by his own admission, lost long before the stage there represented is reached.

Fig. 29 is interesting as illustrating the way in which GOTTE's error as to the origin of the vestibule probably arose The roof of the vestibule, the walls of which are all still undergoing histolysis, is marked off by a clearly defined line from the tissues which separate it from the exterior, and which have recovered from histolysis. In this section the vestibular cavity, which is still narrow, is only cut in a small portion of its course, and in the next section is not seen at all in such a case the line marking the boundary of the histolysed mass might be taken as the margin of the vestibular cavity; and, since it runs down almost to the oral body-cavity, these two cavities might easily be supposed to be in connection with one another (cp. 11, Plate 26, fig. 14)

THE CYSTID.

Since the right and left body-cavities no longer occupy a lateral position, they have been spoken of in the foregoing description as aboral and oral respectively. The use of the words "anterior" and "posterior" in this connection was purposely avoided, partly from the confusion which they would create in comparing my account with those of previous writers, and partly because, as we shall see, they have been, and may still be, applied to very different regions of the body. The oral surface (free end) has always been regarded as ventral, and it would be unwise to alter this nomenclature. CARPENTER, in introducing the alphabetical nomenclature of the radii for descriptive purposes, regarded the anal interradius as posterior: but this arrangement, though almost the only one possible so long as the adult alone is studied, is open to several objections when we come to apply it to the larva. The evidence for these objections will be given later, but obviously the late appearance of the anus makes this structure an inconvenient one to rely upon; and for this reason, as already explained, the interradius of the water-pore is in this paper made the fixed point for the nomenclature of the radii. The other principal objections are —(1) We have reason to believe that the anal interradius is variable; (2) even assuming, as has been done in this paper, that the anus normally occurs in the interradius CD, this interradius is almost ventral in the free-swimming larva (fig. 58), and never at any time has any claim to be considered posterior.

This question, as to which part of an Echinoderm should be considered anterior has already been discussed by LUDWIG for *Asterina gibbosa* (16), and the conclusion arrived at by him, expressed in terms of CARPENTER's alphabetical nomenclature, is that the interradius BC is anterior, supposing, that is, that in *Asterina*, as in *Antedon*, the primary water-pore marks the interradius CD.

Now in the free-swimming larva of *Antedon* the arrangement of the calcareous plates suggests that the præoral lobe is not interradial at all, but in the radius C, and the mouth apparently is in the same radius. Theoretically I should be disposed to agree with LUDWIG that the præoral lobe was interradial, and to regard its radial position in *Antedon* as secondary; but the twisting of the ambulacral and anti-ambulacral fields in *Asterina* makes it a very unsatisfactory subject for the determination of this point: and, until we have further evidence, I prefer to treat radius C as anterior in my description and figures of the pentacrinoid larva of *Antedon*. The change from this to LUDWIG's orientation, if it has to be made, will not be a great one; whereas the adoption of CARPENTER's orientation of the adult would probably lead us far from the truth.

PERRIER's suggestion that the anal interradius should be considered dorsal (19, p. 154) seems to have nothing to recommend it.

The Body-cavities.—The growth towards the *anterior* (formerly ventral) surface of the oral and aboral body-cavities leads to the formation not only of the transverse mesentery, corresponding in part to the oblique mesentery which formerly separated them (cp figs. 59 and 60), but also of two longitudinal mesenteries. The oral (left) body-cavity forms a mesentery in the interradius CD (*oral longitudinal mesentery*), in which, as will be presently mentioned, an important structure, the water-tube* runs. The aboral (right) cavity on the other hand forms a mesentery which is somewhat oblique, being, where it meets the transverse mesentery in the radius C, and at its other extremity, where it joins the stem, in the interradius BC. This is the *aboral longitudinal mesentery.* Its course can be made out from figs. 30 and 31, in which it is cut transversely at two different levels ; and from fig. 35, which shows it in longitudinal section throughout its length.

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* Throughout this paper I have used the name "water-tube" instead of "stone-canal," as the latter is liable to convey the erroneous impression that the tube in question is calcified. The old name has unfortunately been allowed to remain on the plates.

The Water-vascular System.—Hitherto the hydrocele has been spoken of as forming a ring; but it must be remembered that still, as on the seventh day, this ring is incomplete opposite the water-pore. The anterior body-cavity is now, as we have seen, quite small, and lies entirely in the body-wall; and, since it is no longer anterior (except so far as the interradius CD may be considered anterior), it will be better to change its name, and speak of it, as PERRIER does, as the "*parietal canal.*" By the time the cystid phase is reached the hydrocele has cleared itself completely from any histolysis which may have involved it during the previous stages , but both it and its five outgrowths lie completely imbedded in the histolysed mass of cells which form the floor of the vestibule, so that there are at this stage no distinct tentacles (fig. 29). Very soon, however, this mass of cells splits into five broad lobes, which may be looked upon as five primary tentacles ; but as at the same time each of the five primary pouches of the hydrocele splits at its free end into three, we have already the rudiments of fifteen tentacles . at a slightly later period each of these fifteen tentacles projects freely and independently into the cavity of the vestibule.

On the ninth day the epithelium of the hydrocele is very high, and its lumen small ; but the lumen steadily increases at the expense of the epithelium, until by the fourteenth day the latter has become quite flat, while other changes have taken place, which will be described later. The tentacles long retain a more columnar epithelium.

As soon as ever the cystid form is reached the anterior blind end of the hydrocele (see fig. 61) grows aborally and outwards in the oral (left) longitudinal mesentery; in fact, since it is present before the latter is fully formed, it may be looked upon as determining the position of this mesentery. The tube thus formed, which is the equivalent of the " stone-canal " of other Echinoderms, has the same high epithelium as the rest of the hydrocele ring, and it retains this character throughout, instead of sharing in the changes which the main part of the hydrocele subsequently undergoes. After entering the body-wall it turns slightly towards the oral surface, and on about the tenth day opens into the parietal canal (anterior body-cavity) (fig. 30). The course of the communication thus established between the hydrocele and the exterior is somewhat complicated, but can be traced in figs. 32, 33, and 34, which are taken from a series of transverse sections of a larva of the twelfth day, starting from the oral surface. In fig. 32 the edge of the water-pore is cut, together with the commencement of the parietal canal and of the water-tube. Owing to a slight obliquity in the plane of section, the lower wall of the water-vascular ring is cut on one side of the water-tube; while on the other side (in the radius D) the section passes through the base of one of the tentacles. Several sections intervene between this and fig. 33, in which the water-tube opens into the parietal canal, as will be seen, the whole of the former and part of the latter lie in the oral longitudinal mesentery, which separates the two ends of the oral body-cavity.

After two sections more we come to that represented in fig 34, which shows the continuation of the parietal canal below the water-tube. On one side of the oral longitudinal mesentery the section passes so low that it exposes the aboral longitudinal mesentery, lying in the radius C; and between the two longitudinal mesenteries is an open communication between the oral and aboral body-cavities, where part of the transverse mesentery has already broken down. Towards the radius D the transverse mesentery is seen joining the oral longitudinal mesentery.

During the transition to the cystid stage the walls of the parietal canal share in the general histolysis, but in the earliest stage of the true cystid it has recovered from this, its lumen is quite distinct, and it is bounded by a cubical epithelium, which is, however, quite distinct from the epithelium of the water-tube (fig 33). The epithelium of the pore does not at this stage materially differ from that of the parietal canal; but subsequently the epithelium of the latter flattens out, while that of the former remains cubical, and spreads somewhat further in from the surface.

The Alimentary Canal.—Late on the eighth day the alimentary canal, which is completely filled with cells, and whose true epithelium is with difficulty, if at all, distinguishable, is flattened or slightly concave towards the interradius CD. Almost immediately after its formation that part of the transverse mesentery which lies along this concave side of the alimentary canal, between the oral and aboral longitudinal mesenteries, breaks down, and so establishes the free communication between the oral and aboral body-cavities, which has already been mentioned in describing fig. 34. A remnant of this part of the mesentery is still seen in fig. 30. At the same time the concavity of the mesenteron increases greatly, so that it assumes a crescentic form. One horn of the crescent is blunt, and remains connected with the floor of the vestibule; but the other horn, which is more tapering, loses all direct connection with the vestibule, and runs in the transverse mesentery to join the body-wall in or near the radius C, the aboral mesentery joining its lower border; it acquires a columnar epithelium, and forms the rectum, but does not open to the exterior till a considerably later period.

The blunt horn of the crescent becomes hollowed out by a funnel-shaped depression, which grows down from the vestibule, and round which a high columnar epithelium is developed. This depression (marked "*stomodæum*" in figs 32–34) is, as LUDWIG remarked (14), eccentric, being in the interradius CD; and this eccentricity becomes more and more marked as the disc increases in size.

The alimentary canal now consists of three distinct regions; (1) stomodæum, (2) stomach, (3) intestine. By about the fifteenth day the stomach has developed a cubical or low columnar epithelium, and its cavity, which has now nearly got rid of its cellular contents, communicates by means of the stomodæum with the vestibule.

The roof of the latter has by this time become very thin, and shortly afterwards splits into five lobes in the well-known way, and places the cavity of the alimentary canal in direct communication with the exterior

The Body-wall and Stalk—As already mentioned, the commencement of the cystid stage is marked by the transparency of the superficial tissues; and this is due to the recovery of these tissues from histolysis (fig. 29). Moreover, we noticed that all round the larva there was a narrow hyaline border, in which were imbedded the pyriform "yellow-cells," and in which more careful observation shows us, especially at a later stage and in the stalk, thin strands of granular protoplasm belonging to other cells, and set perpendicularly, or nearly so, to the surface of the body. We might naturally suppose that this hyaline border was the ectoderm; but sections show us that, so far from this being the case, this border only marks the average limit of the nuclei; and, though in many places there is a more or less marked row of cells sending processes through the hyaline border to the exterior, yet these cells are not everywhere present, and are never marked off distinctly from the subjacent mesoderm (fig. 29). In fact there is no distinct superficial layer which we can speak of as the ectoderm; and the term seems only applicable to the cells bounding the water-pore, and to the mass surrounding the vestibule; and even the latter in places usually passes insensibly into the mesoderm (fig. 29), and at a later stage (fig 35) is largely replaced by mesoderm, so that no part of the vestibule except its floor has a distinct epithelial lining

A detailed description of the histology of the stalk has been given by PERRIER (19, p. 133).

The Chambered Organ and Axial Organ.—While the mesoderm was undergoing histolysis the cavities of the chambered organ were no longer distinguishable, but now, with the recovery of the tissues from the histolysed condition, they reappear as before in open communication with the aboral body-cavity. We have already seen that the aboral longitudinal mesentery, where it joins the stem, lies in the interradius BC. The present arrangement therefore of the chambered organ is that represented in fig. 57, and this diagram will also serve to explain why in the free-swimming larva it was assumed that the ventral (now anterior) chamber arose from the body-cavity on the left-hand side (cp. fig. 56). Very shortly after the cystid stage is reached the chambered organ becomes completely shut off from the body-cavity by means of thin transverse partitions, whose origin I have not been able to trace satisfactorily. In fig. 29 one of the chambers is seen still opening to the body-cavity, but in fig. 35 they are completely closed, and appear to end blindly in the base of the longitudinal mesentery.

It has already been mentioned that the central core round which the chambers are grouped represents the rudiment of the axial organ. It had not indeed any distinct structure at the previous stage, but as soon as the cystid phase is reached it begins to grow up into the lower part of the longitudinal mesentery, where it forms a cord of cells especially conspicuous in transverse sections As it grows higher up towards the oral surface it leaves the mesentery and pushes its way under the peritoneal epithelium into the position seen in fig. 31. This change will be better understood by reference to figs. 36 and 37, where the transition is represented on a large scale, fig. 36 being at the same level as fig. 31. In what has generally been described under the name of axial organ, Perrier rightly distinguishes two parts—(1), which he calls the "stolon génital," consisting of cells with large deeply-staining nuclei; and (2), the sheath of this organ. It is to the former that I have confined the term "axial organ," as the latter appears to me to be at first nothing more than the peritoneal covering; for, though in figs. 36 and 37 we see something of an additional sheath, this does not appear to me to take any part in the subsequent changes that Perrier attributes to the sheath of the "stolon génital," but to remain closely connected with this stolon. The true axial organ ends off by the side of the œsophagus at about the level of the transverse mesentery, but its sheath, the cells of which are somewhat different from those of the rest of the peritoneum, is seen in longitudinal sections to run up as far as the floor of the vestibule. The axial organ itself appears to grow up from the stem, and therefore to be mesodermic; Perrier speaks of it as "d'origine entodermique" (19, p 163), but by this he appears to mean nothing more than that it is derived from the splanchnic peritoneum, which he believes to be continued into the stem

We have now traced the organogeny of the cystid up to the time that the vestibule opens to the exterior. Many points in its anatomy have been correctly described by previous observers, and have only been introduced here for the sake of clearness; but in other points the preceding description differs considerably from those of previous writers; and to the discussion of these differences we must now turn our attention.

That the two longitudinal mesenteries have hitherto escaped notice is, I believe, due to the fact that neither Gotte, Ludwig, nor Perrier cut transverse sections. So far as these two mesenteries were seen by these observers, they appear to have been either confused with the axial organ, or explained in some other way. Thus Perrier (19. p. 142) describes the oral body-cavity as pushing its way down in the angle of the alimentary canal, and so driving before it that part of the tranverse mesentery which I have described as breaking down. To him, therefore, the cavity into which the axial organ projects is part of the oral body-cavity, while to me it is part of the aboral cavity, freely open above to the oral cavity. But the process described by Perrier should lead to the formation of *two* aboral longitudinal mesenteries, whereas transverse sections clearly show that only one is present (fig. 31).

Part of the oral longitudinal mesentery was undoubtedly seen by Ludwig, who regarded it as an incomplete partition separating off that part of the body-cavity into which the water-tube opens (14, p. 38). To Perrier is due the credit of correcting Ludwig's statements with regard to the water-tube, and denying its connection with the oral body-cavity. But, though I fully agree with Perrier in this point, I am compelled to differ from him in regard to details. He describes a single "tube hydrophore" leading from the hydrocele ring to the water-pore, and having in the early cystid stages the same structure throughout its course, though at a later period the part within the body-wall (parietal canal) has a thinner epithelium than the "partie libre" (water-tube). To me there is from the first a distinct difference between these two parts, corresponding to their distinct origin . while the so-called "partie libre" lies throughout its course in the oral longitudinal mesentery. Moreover PERRIER describes this "tube hydrophore" as forming a simple U, and in Plate I., fig. 9, he figures its lumen as cut throughout its length in a single section. My researches do not lead me to regard such a section as possible. The course of the two cavities is shown in figs. 32, 33, and 34, and seems to me closely to correspond with LUDWIG's description of it (14, p. 38), except that there is a closed parietal canal in place of his cavity L′ opening to the oral body-cavity (cp also 19, fig. 16)

The rest of PERRIER's description, especially the histological part, is extremely good ; but I cannot accept his view that the axial organ is a tightly stretched cord, which forces the alimentary canal to assume a spiral arrangement. Not only is this view unintelligible phylogenetically, but transverse sections would have shown him that, in most of its course, the axial organ does not lie in the angle of the alimentary canal, and is therefore not in a position to produce the effect which he supposes.

To his description of the later stages of the cystid, subsequent to the rupture of the vestibular roof, I have little to add; but it may be as well to give a brief sketch of the principal changes which occur.

The whole floor of the vestibule, as well as the œsophagus, is lined by ciliated columnar epithelium. The walls of the stomach are formed by high columnar cells, the free ends of which are merged (in sections) in a structureless granular mass (fig. 39). PERRIER attributes this to the extreme delicacy of the cells, causing instant decomposition after death ; but I am more inclined to regard this mass as a form of secretion from the cells than as due to bad preservation ; and I may call attention to the fact that W. THOMSON (21, p. 525) described glandular folds in the stomach, of which he says, "the slightest touch, even of a hair, ruptures them and causes the effusion of a multitude of minute granules, some colourless and transparent, and others of a yellow or brownish hue." I regret to say that I made no observations with respect to this point on the living animal. It is also possible that these granules are the last traces of the histolysis : at a later period the margins of the cells are often quite easily seen, and are clothed with long cilia.

Very soon after the rupture of the roof of the vestibule the anus opens to the exterior, and the alimentary canal at once becomes filled with the siliceous skeletons of diatoms, &c., which render the cutting of thin sections almost impossible. LUDWIG, as the result of the examination of "mehr als hundert Larven" (14, p. 44), asserts that the anus opens, not in the same interradius as the water-tube, but, following the curvature of the alimentary canal, in the one before it, *i.e*, on the nomenclature here adopted, in the interradius B C. This is a point of considerable importance, but I cannot but think that LUDWIG is mistaken, and that here again transverse sections would have led him to a different conclusion. From longitudinal sections, or from whole larvæ made transparent, such as LUDWIG used, I have been totally unable to arrive at any certainty on this point; but in series of transverse sections the radii are clearly marked, and the relations of all the organs to them can be seen at a glance.

Not counting numbers of such series before the appearance of the anus, in all of which the rectum joins the body-wall, either in the radius C or in the interradius C D (figs. 30 and 34), I have series of transverse sections through more than twenty larvæ, in which, with a single exception, the anus and water-tube most certainly lie in one and the same interradius. Since the two are at different levels, this point is usually only seen by looking through a series of sections; but in fig 38 a section is represented which, by a fortunate obliquity, shows both anus and water-tube at once The exception above mentioned is interesting. In one of my larvæ the anus does lie in the interradius B C, but close to the radius C; and, if LUDWIG's suggestion be true, that the anal interradius is not homologous in all Echinoderms, but that the position of the anus has undergone a phylogenetic change, this exception may be looked upon as a case of reversion to a condition which is permanent in the Asterids. In any case this exception does not affect the conclusion that the anal interradius in *Antedon* is normally the same as that of the water-tube; while it justifies me in making the latter, rather than the former, the standpoint for the nomenclature of the radii.

PERRIER unfortunately throws no light upon this point; he simply describes the alimentary canal as making "un tour de spire complet" (19, p. 141), which seems to support my account; but he says nothing about the radii, and if he had been aware of Ludwig's error, he would surely have mentioned it.

The stomach, which in the previous stage was thick and extended almost to the centre of the body, is now much thinner, and the alimentary canal winds as a spiral round a well-developed axial cavity (fig. 39). The axial organ, however, still retains a central position, and to enable it to do this the peritoneal epithelium covering it is pushed into a mesentery, which, however, does not reach the body-wall.

The cells of the axial organ, at first grouped irregularly, now range themselves round a central cavity, but, up to the time of the formation of the arms, the organ does not usually undergo any further complication.

Late in this stage the mesenteries begin to break down; the aboral one is the first to go (fig. 39), but the transverse mesentery soon follows, though both continue for some time to be represented by fibrous bands running at intervals from the alimentary canals to the body-wall. Other similar bands are also developed independently of the mesenteries, especially between the floor of the vestibule and the œsophagus.

The water-vascular system really changes considerably just before the end of the last stage; but the description of these changes has, for convenience, been left till now.

The water-vascular ring closes completely, and about the same time a number of muscular (?) threads appear, which traverse the lumen of the vessel These threads appear to me to be nothing more than processes of the ordinary cells of the epithelium, which has now become extremely thin. At a later period the nucleus shifts into the middle of the thread, which then appears to be a single cell, with a protoplasmic core surrounded by a formed substance (fig. 41). LUDWIG, however, describes them (13, p. 17) as being composed of a central muscular thread, covered by a thin epithelial layer, derived from the epithelium of the water-vessel.

About the time of rupture of the vestibule the number of tentacles increases to twenty-five, which, however, are still arranged in five radial groups.

The epithelium of the parietal canal flattens out, and gradually fuses with the surrounding mesoderm, so as to be no longer recognisable. At the same time a very distinct epithelium grows inwards for a certain distance from the water-pore, but never reaches the expanded part of the parietal canal shown in fig 33. We have now an arrangement which closely corresponds with that seen in other Echinoderms. *e.g*, in Ophiurids (cp. 15, Plate 14, fig 1), in both the water-vascular ring communicates with the exterior by means of the following structures —(1) a water-tube, with a columnar epithelium; (2) a swollen part, with a flat epithelium, called the *parietal canal* in *Antedon*, and the *ampulla* in Ophiurids; (3) a pore-tube with columnar epithelium ; (4) a water-pore.

The two vessels, supra-intestinal and sub-intestinal, described by PERRIER (19, p. 143), are very conspicuous long before the end of the cystid stage, and can be traced into connection with one another at the base of the aboral mesentery, but they do not appear to have any connection yet with the chambered organ.

In the latest stages examined by me the nervous system was not yet clearly developed.

The peritoneal epithelium covering the alimentary canal remains distinct up to the end of the cystid stage, but the somatic peritoneum usually fuses with the body-wall at a very early period. The outer wall of the water-vascular ring, too, completely loses its epithelium, which, as was noticed by PERRIER (19, p. 150), fuses with the mesoderm of the body-wall (fig. 41).

The whole exterior, except the floor of the vestibule and the tentacles, remains entirely destitute of ectodermal covering, and this I believe to be equally true of the adult. The walls of the water-pore are probably ectodermic, and the ambulacral epithelium of the arms is certainly so, being directly derived from the floor of the vestibule, but elsewhere I can find no true ectoderm. PERRIER describes a flat epithelium in the adult (18, p. 50), though he cannot find it in the larva (19, p. 125); and VOGT and YUNG also speak of a flat epithelium (22, p. 532), but I do not feel sure that they are not simply following PERRIER.

That an epithelium appears in surface views to exist in some parts I willingly admit, but in section we see that the superficial cells are in no way marked off from the mesoderm , and on the dorsal surface of the pinnules and arms no appearance of an epithelium is visible, even in surface views, the cells being separated by considerable intervals, and the surface being formed by a strong non-cellular membrane (see PERRIER's excellent figure, 18, fig. 11). This conclusion is completely borne out by nitrate of silver preparations (HARMER's method); at first sight they sometimes appear to show an epithelium, but in most parts no silver lines mark out the limits of the cells, and in all cases careful focussing shows that the nuclei are at very different levels, so that the epithelium, even if present, is certainly not flat.

Two points remain to be described which were purposely omitted from the foregoing account of the cystid.—(1), the Sacculi; (2), the Skeleton.

The Sacculi.—Before giving an account of the development of these bodies, it may be well to describe their structure in the adult, so far at least as it is known. The only good description and figures of them that I have been able to find are those of PERRIER (18), but his account does not seem to have received much attention. Each sacculus is a spherical body, bounded by a thin membrane, in which are imbedded a few flattened nuclei. The interior of the sphere is more or less filled with a number of pyriform sacs, each of which in its turn is filled with highly-refractive spherules, and is bounded by a membrane, continued at its inner end into a long thread, which joins the wall of the sacculus. One of these pyriform sacs, with its process, is seen in fig. 42(*c*). The refractive spherules, which usually take up colouring-matter with great avidity, have, at any rate in some cases, a definite arrangement round a central cavity. Two such sacs are shown in transverse section in fig. 43. The spherules, which are spherical when isolated, are evidently much compressed within the sacs. On the wall of each of these pyriform sacs PERRIER describes a small nucleus; but this point I have not yet been able to confirm, though the peculiar optical properties of the spherules, and the readiness with which they stain, render the investigation of this point a matter of no ordinary difficulty, and make the negative evidence afforded by my observations of little importance.

The greater part of the sacculus is imbedded in the tissues, but at one point its cavity is only separated from the exterior by its limiting membrane, which at this point stains deeply, and does not exhibit any nuclei (see the diagram, fig. 44). During life the sacculus has a swollen appearance, and its free margin frequently bulges out towards the exterior; this is due to the presence of a quantity of mucus between the pyriform sacs and the wall of the sacculus; and, if a living pinnule be placed on a slide with a drop of water, this water becomes charged with mucus; though whether this is due to a continuous secretion, or to injury to the pinnule, I am unable to say. Any rough treatment, however, of the pinnule leads to the escape not only of increased quantities of mucus, but also of many of the spherule-bearing sacs. In spite of this, it is rare to find in sections a sacculus freely open to the exterior, and I can only suppose that there is some means of rapidly mending the ruptured membrane.

Let us now turn to the development. The first rudiments of the sacculi appear on about the tenth day, as five small bunches of cells situated at the radial angles of the water-vascular ring In this position they were recognised at a later stage by W. THOMSON (21, Plate 26, fig. 1, &c.) and by LUDWIG (14, Plate 12, fig. 2), and it is, therefore, surprising to find PERRIER (19, p 150) stating that they *alternate* with the groups of tentacles, especially as this is opposed to his own figures (19, Plate 2, fig. 16). Each of these groups of cells really has the form of an epithelium surrounding a small slit-like cavity. The side of the organ towards the water-vessel remains flattened, but the outer face soon becomes convex, and so increases the size of the central cavity. At the same time certain cells are pushed out into the central cavity from the flattened side (fig 40). In sections these cells appear to lie quite freely in the cavity, but I have very little doubt, from what I have seen in later stages and in macerated specimens, that they really remain connected with the epithelium by a fine process; and, indeed, some indication is given of this in fig. 40.

At first the nuclei of the cells composing the epithelium are indistinguishable from those of the surrounding mesoderm, though those of the cells within the cavity are somewhat larger. Very soon, however, all the cells of the sacculus undergo considerable changes, so that by about the twelfth day their contents stain almost as readily and deeply as in the adult. Fig. 41 shows the appearance of a section through a sacculus on about the twentieth day. The spherule-bearing sacs are developed much as in the adult; though, in correspondence with the small size of the sacculus, they are much fewer in number and smaller in size; being for the most part cut obliquely, they show neither the central cavity nor the thread-like continuation at the base, but the latter can be seen in teased preparations (fig. 42, *b*). From their size it might be supposed that each spherule was derived from a single cell, and, perhaps, even from the nucleus of that cell, but a careful examination of the cells composing the wall of the sacculus makes this improbable. It will be seen (fig. 41) that the epithelium of this wall is already much flatter than in the previous stage, though by no means so thin as in the adult. Each cell of this epithelium contains several refractive spherules, similar in character to those in the central cavity, but smaller in size than most of them ; and besides these each cell bears a nucleus, which is, however, much reduced in size and obscured by spherules. From the analogy of these cells I was led to believe that each spherule-bearing sac (not each spherule) represented a single cell, which had become greatly enlarged, and whose protoplasm had broken down into spherules of some formed matter. This conclusion is borne out by the examination of teased preparations of larvæ at various ages (fig. 42, *a* and *b*); but between the earliest stage of the refractive spherules (fig. 42 *a*) and the cells represented in fig. 40 I never succeeded in finding any intermediate form.

The cells of the central cavity alter in their chemical and optical properties before those of the epithelial wall: and it was probably this that led PERRIER to describe the sacculus in its earliest stage in the regenerating arms as consisting solely of a few refractive spherules, without any definite wall (18); it was hardly likely that he would detect this wall without sections before it began to stain differently from the rest of the mesoderm.

My investigations on the subsequent changes undergone by the sacculi are still far from complete; but I have frequently noticed a few quite young spherule-bearing sacs in a fully developed sacculus of the adult; and I have some reason for thinking that these sacs break down and form the mucus which distends the sacculus.

Several suggestions have been from time to time made as to the possible function of these organs; but the most obvious one, that they are excretory, has generally been given up, because no external opening has been found. I have little doubt that one of their functions is to secrete mucus; though whether this mucus is simply protective, or whether any waste products are got rid of with it, I am unable to say. it is quite possible, however, that more than one function may be performed by them.

One suggestion, however, as to their nature cannot be passed over in silence. They have recently been described by Vogt and Yung (22, p. 570) as collections of algoid zoospores; and the amœboid spores of these Algæ are supposed to enter the free-swimming larva in the form of "yellow-cells." Dr. P. H. Carpenter has already discussed these statements (8), and has shown strong reasons for doubting them; and to his arguments I will now add others.

Vogt and Yung's theory involves three distinct questions, which we shall do well to consider separately: (1) Are the "yellow-cells" amœboid spores of Algæ? (2) Are the sacculi zoospores of Algæ? (3) Have the yellow-cells and sacculi anything to do with one another?

(1.) The colour of these cells when seen by transmitted light is certainly suggestive of chlorophyll; but, of course, there are many other green colouring matters, and I unfortunately had no opportunity of applying the spectroscope to these cells. Their appearance in the free-swimming larva has already been described. In the later stages, and in the adult, they are, so far as I know, always superficial, and, when decolorised, indistinguishable from the cells surrounding them; indeed I am strongly disposed to agree with Perrier that the ordinary connective-tissue cells and these yellow-cells "sont morphologiquement de même nature, que ces derniers ne diffèrent des autres que parce que la matière jaune a envahi tout l'intérieur de la cellule et distend ses parois" (18, p. 53). The objections, then, to regarding these cells as amœboid spores of Algæ may be summed up as follows:—

(*a*) They appear before the rupture of the vitelline membrane.

(*b*) They acquire their colour gradually.

(*c*) They closely resemble the surrounding cells in all points except colour.

(*d*) They are always superficial.

(*e*) They exhibit no amœboid movement.

As far as I am aware, the vague possibility that the colouring matter of these cells may be chlorophyll is the only point of support for this part of Vogt and Yung's theory.

(2) This part of the theory is to me even more incredible than the last. VOGT and YUNG state that certain "paquets de granules réunis ont, suivant M. PERRIER, des queues très longues et déliées, ce sont donc de véritables zoospores" (22, p. 570). That certain "paquets de granules" do exist buried in the tissues of the adult I willingly admit, but they have no sort of resemblance to the true sacculi, and the account given above of the development of the latter is entirely opposed to the supposition that they are formed by collections of these granules. Moreover, the fine processes of the spherule-bearing sacs were described by PERRIER as joining the wall of the sacculus; they exhibit no amœboid movement, and are not in the least suggestive of flagella.

But the strongest argument of all against this part of VOGT and YUNG's theory is the fact that during life the contents of the sacculi are *absolutely colourless,* which is entirely inconsistent with the statement that they are algoid zoospores Yet this fact should have been well known, since it has been frequently mentioned (21, p. 527, 6, p. 127; 18, p. 67).

(3.) It is impossible absolutely to prove that the yellow-cells and sacculi have no connection with one another; but their extremely different appearance in the living animal and the entire absence, so far at least as my observations go, of any intermediate structures between them render such a connection so highly improbable, that the onus of proof must rest with Messrs. VOGT and YUNG.

The Skeleton —As already mentioned, the number of stem-joints in the free-swimming larva is variable, but by the time the larva fixes itself from thirteen to fifteen are usually present, and this number is maintained throughout the pentacrinoid stage. Very shortly after fixation all the stem-joints in succession, beginning with the most anterior one, form complete rings, the closure being of course in the radius C; and at the same time longitudinal processes spring from them at a short distance from the inner margin, while the horizontal processes already noticed anastomose, so as to increase the diameter of the plate: such a plate with rudimentary longitudinal processes is seen in fig, 51. New longitudinal processes now arise from this network, which again anastomose freely with their fellows; and in this way the structure of each stem-joint becomes very complicated. Each consists of a transverse plate, from each side of which arise a number of longitudinal rods, united among themselves by cross anastomoses; and the transverse plate, which marks the middle of the joint, projects both externally and internally (*i.e.*, towards the hollow axis) slightly beyond the longitudinal rods (fig. 46). The origin of these longitudinal rods has been misunderstood by both THOMSON (21, p. 523) and GOTTE (11, p. 495), who regard them as bundles of rods arising, not *from* the ring, but *within* it, or, in THOMSON's words, as "a hollow sheaf of parallel calcareous rods . . . as it were, *bound* in the centre by calcareous rings."

By the elongation of the stem-joints the dorsocentral plate is rapidly driven forwards into the disc of attachment, where it remains as a circular, and afterwards pentagonal, plate, which undergoes no important changes.

The oral and basal series of plates, which were oblique in the free-swimming larva, now assume a transverse arrangement, in correspondence with the transverse position of the mesentery separating the oral and aboral body-cavities. At the same time they increase greatly in size, though not much in thickness (figs. 46 and 49), and soon fill up the wide gap which formerly existed in the radius C. One of the oral plates envelopes the water-pore.

But by far the most interesting skeletal changes at this stage are connected with the three underbasals. The inner border of each of them soon becomes smooth and concave (fig 50), and they then range themselves in a circle around the chambered organ, just above the top stem-joint. Two of them are seen in a cystid of the tenth day in fig. 46; but their relation to the radii is better seen in fig. 48; in this section the top stem-joint is seen lying immediately under the underbasals, and the closing point of this ring-like joint, still faintly indicated, marks the radius C, which, of course, can also be determined by following the series of sections. One of the previous sections is indicated by a dotted line, in order to make the positions of the radii more evident. We now see that the arrangement of these plates is still the same as in the earlier stage, the smallest plate being in the radius A. At a slightly later stage these three plates fuse with one another and with the top stem-joint, so as to form one large plate, which is represented as seen from the aboral side in fig. 52, and in side view in fig. 53. It will be seen that, though the sutures of the underbasals still persist, the plates themselves have grown out into five angles. These angles are radial in position, fitting in between the bases of the basal plates; and, while the underbasal of the radius A produces only one angle, each of the other two grows out into two angles: this fact strongly suggests that each of these larger underbasals represents a pair of coalesced plates, and that the primitive arrangement would be the possession of five radial underbasals. At a slightly later stage the sutures disappear, though the groove separating the underbasal series from the top stem-joint persists for some time. The whole large plate thus formed has always been regarded hitherto as a simple centrodorsal, whereas, in reality, the top stem-joint, forming only the lower half of this large plate, is the true centrodorsal. But, though agreeing in regarding this large plate (underbasals *plus* centrodorsal) as a simple centrodorsal, previous writers have differed somewhat as to its mode of origin. WYVILLE THOMSON described it as a modification of the top stem-joint, but suggested that it represented "a coalesced series of nodal stem-joints in the stalked Crinoids" (21, p. 536); and this view was adopted by W. B. CARPENTER (10, p. 737). GOTTE, however, regards it as arising from the fusion of certain small plates (number not mentioned) developed in quite a different region from the youngest stem-joints, and surrounding the stem at some little distance from its growing point. In the deformed specimen which he figures (11, fig. 50) it is very probable that he actually saw one of the underbasals; but in his description and his fig. 13 he appears to refer to something quite different, possibly to broken pieces of the basals; for, as I have shown, the underbasals do not surround the stalk, but are developed close to its growing point, and if any part of it is overlapped by the basals, the underbasals are overlapped by them too (fig. 45); moreover they are developed at a much deeper level than the basals, and one at least of them is radial.

Perhaps it will be well before proceeding further to give reasons for regarding the three plates which I have described as underbasals, and not as parts of the centrodorsal, as GOTTE has done. Of course, if there had been five plates instead of three, and these plates had all been radial, there could be no question about the propriety of this nomenclature; and the facts above related are strongly in favour of regarding these three plates as representatives of five radial plates But it is not on this alone that I have relied. Some of the dicyclic Palæocrinoids (*e.g.*, the Ichthyocrinidæ) have throughout life three instead of five underbasals, one of which is smaller than the others, and in some forms it is situated anteriorly, opposite to the anal interradius; so that these three plates have precisely the same symmetry as those in *Antedon*. Moreover, Dr. CARPENTER informs me that in the structure of the arms and rays the family Ichthyocrinidæ more nearly approaches the Comatulæ and Pentacrinidæ than do any of the other palæozoic Crinoids.

I cannot attempt to discuss in full the importance of this discovery of underbasals in *Antedon* on the classification of the Crinoidea, but attention must be called to the somewhat curious way in which it confirms the generalisations of WACHSMUTH and SPRINGER (23). As a result of their admirable researches among the Palæocrinoids, these observers find that the presence of underbasals is so invariably correlated with the existence of interradial angles in the stem that these angles may be taken as an indication of the existence of underbasals, even when the latter are invisible on the surface. They then state that, as regards the stem, the Neocrinoids are "built upon the plan of the dicyclic Crinoids" (23, Sect. I, p. 71), although hitherto they have been regarded as monocyclic; and, after pointing out that in all Comatulæ the angles of the centrodorsal are interradial, they add, "upon this mainly we base the opinion that perhaps also the Comatulæ in their early larvæ had rudimentary underbasals" (23, Sect. II., p 222). Against these generalisations CARPENTER (9) raised what certainly appeared to be insuperable objections: firstly, that many of the Neocrinoids (*e.g.*, *Apiocrinus*) were not "built upon the plan of the dicyclic Crinoids," but had radial angles to the top stem-joint: and, secondly, that in the larval *Antedon* also the angles of this plate were at first radial, the interradial angles which it possesses in the adult being due to a secondary growth. Now, however, we learn that the underbasals are really present all the time, not, as WACHSMUTH and SPRINGER suppose, "hidden by the column" (23, Sect. I., p. 293), but actually visible in the larva of *Antedon*, as the radial angles of the so-called centrodorsal; and that the true centrodorsal (= top stem-joint), with which the underbasals are indistinguishably fused, either remains without angles, or by a later growth develops radial angles, and at the same time overlaps and conceals the underbasal angles.

The remaining changes in the skeleton are already so well-known from the works of WYVILLE THOMSON (21) and W. B. CARPENTER (10) that no further description need be given here.

GENERAL MORPHOLOGY.

It is now time to justify the adoption of BARROIS's theory with regard to the orientation of the larva. In the first place, let us consider what are the grounds upon which the old orientation was based; they may be briefly summed up as follows:—

(1.) WYVILLE THOMSON, with peculiar theoretical opinions on the subject of larval forms, named the larval mouth the "pseudostome," and the præoral pit the "pseudoproct," and fancied he could distinguish an alimentary canal joining them. This view needs no comment.

(2.) The mouth, assumed to be anterior, ultimately appears at the pole opposite to that by which the animal fixes itself, and this is probably the main reason why the stalk has been regarded as posterior. We know, however, that many larvæ (Ascidians, Cirripedes, Polyzoa) fix themselves by the anterior end, and afterwards rotate the mouth round to the opposite pole

(3.) GOTTE described the œsophagus of the pentacrinoid as surrounded by the *left* body-cavity, as is the case in other Echinoderms; and this, if true, would form a strong objection to BARROIS's views. BARROIS, however, escapes from this difficulty by regarding the right and left body-cavities as retaining a lateral position; but this view involves a belief in a remarkable difference between the Crinoids and the other Echinoderms—an objection which BARROIS ignores. For my own part, as already stated, I am convinced that the two body-cavities do not remain simply right and left, but that, on the other hand, the shifting which they undergo is such as, on the old orientation, to bring the *right*, and not the *left*, cavity into an oral position in the cystid. Only by adopting the new orientation can we bring the Crinoids into correspondence with other Echinoderms on this point.

(4.) GOTTE described the anus as appearing on what was originally the ventral side; it is true that it is not actually in the radius C, but it is so near it that it may be described as lying almost exactly between the mouth and what BARROIS has called the præoral lobe. Here then we encounter a really serious objection to BARROIS's theory, and one which, if his account of the body-cavities were accepted, seems to me absolutely insuperable. It would be interesting to know how BARROIS himself meets this difficulty, but unfortunately in his brief note he makes no mention of it at all.

But if the account of the body-cavities given in the preceding pages of this paper be accepted, the position of the anus does not seem to me to place any real difficulty in the way of regarding the fixed end of the larva as the præoral lobe. LUDWIG has already discussed the position of the anus in Echinoderms at considerable length, and with his usual ability (14); and he has come to the conclusion that, while the interradius of the water-tube is probably constant, that of the anus varies in the different groups Thus, if we make use of the nomenclature adopted in the preceding pages, and call the interradius of the water-tube CD, then the anal interradius will be in Holothurians and Echinids AB, in Asterids (but not in Crinoids, as LUDWIG thought) BC, and in Crinoids CD, showing a progressive shifting of its position up to the last group. The curvature in the course of the alimentary canal to which this shifting leads is, as LUDWIG pointed out, already shadowed forth in the bilaterally symmetrical larvæ of most Echinoderms in the curvature of the alimentary canal towards the ventral surface; and the shifting of the anus appears to take place along this ventral side, in the mesentery separating the right and left body-cavities.

Let us now see how this affects the case of the larva of *Antedon*. The analogy of other Echinoderms justifies us in supposing that the blastopore represents the anus; and, indeed, this assumption forms the main point of BARROIS's argument. We are not here directly concerned with the question whether the blastopore is terminal, or a little dorsal or ventral · it is enough for our present argument that both BARROIS and myself are convinced that it is somewhere near the pole which we have called posterior —nearer to it than is the larval mouth. This being so, let us imagine the anus shifting its position along the line of the mesentery separating the right and left body-cavities If these cavities retained their lateral position, the anus would continue ventral, and could only move forward as far as the larval mouth. But these lateral positions are not retained, and, if at the time of shifting of the body-cavities the anus was on the ventral side, then the anus, with the ventral mesentery, would be shifted over on to the right side of the larva. I have not been able to represent this clearly by diagrams, but a little consideration will show that the mesentery represented in fig 59 had originally a ventral position, and the anus may be imagined to lie in it In this figure the mesentery is oblique, but after the rotation of the mouth to the posterior pole this oblique mesentery becomes transverse, and grows completely round the larva. There is nothing then that I can see to prevent the anus from continuing to migrate along the line of the mesentery, until it not only reached, but even passed, the radius C, in which the mouth formerly lay, so that, instead of stopping, as it does in Asterids, in the interradius BC, it might reach the interradius CD, in which we find it in the pentacrinoid stage of *Antedon*: and this view is to some extent supported not only by the exceptional case already mentioned, but also by the fact that the rectum, before the appearance of the anus, is attached either in the radius C, or at any rate nearer to it than the future anus is.

If once the possibility be admitted of the shifting of the anus along the mesentery, I do not see that any strong objections can be raised against the above hypothesis; but I confess that I should never have put this hypothesis forward if I had not been led to doubt the correctness of the old orientation by the fact that it necessitates a belief in very great differences between Crinoids and other Echinoderms.

Let us now for a while assume the correctness of the old orientation—let us suppose that the larva swims backwards and fixes itself by its posterior end, and see what these differences are. They may be summed up as follows :—

(1.) The blastopore closes at or near the anterior end. In all other Echinoderms it either closes posteriorly or persists as the anus.

(2.) The first rudiment of the hydrocele appears at the posterior end of the right body-cavity (though not connected with it). In all other Echinoderms it is at the anterior end of the left body-cavity, from which it is usually derived.

(3.) The water-pore is on the right side, posterior to the right body-cavity. It is usually on the left of the middle dorsal line, anterior to the left body-cavity.

(4.) In the later stages the right body-cavity surrounds the œsophagus; in all other Echinoderms it is the left body-cavity which does this.

(5.) Looking at the animal from the side on which the right body-cavity lies, the alimentary canal winds round in the same direction as the hands of a watch; whereas, as LUDWIG has shown, the same direction for the winding of the alimentary canal is obtained in other Echinoderms, even in the bilaterally symmetrical larvæ, by looking at them from the left side.

These facts afford, I think, an almost overwhelming proof that the old orientation is wrong; but, as a final argument in favour of BARROIS's theory, I will show what a close comparison it enables us to make between the larva of *Antedon* and that of *Asterina gibbosa*, as described by LUDWIG (16). In doing this, however, I am compelled to differ somewhat from LUDWIG's nomenclature of the parts of the larva, which he gives on p. 143, since I regard the mouth as ventral, and the whole of the larval organ as anterior, representing the præoral lobe.

With regard to the external form not much can be said. but in both types the larval mouth lies in the middle of the ventral surface, and in both there is a large præoral lobe; and it is perhaps not extravagant to compare the large sucker of the præoral lobe in *Asterina* with the "præoral pit" by which the larval *Antedon* fixes itself.

In the internal anatomy the resemblance is more striking, as I have endeavoured to show in the two diagrams (figs. 61 and 62). In both these figures we are supposed to be looking at the larva from the side on which the hydrocele lies, which is already the oral side in one, and will be so later in the other.

In *Antedon*, at one stage at any rate, there are four separate cœlomic pouches; and, though in *Asterina* there is only one, yet this is partially divided into four, which closely correspond with those of *Antedon*. In the first place we have in both an anterior unpaired body-cavity, occupying the whole or part of the præoral lobe, and opening to the exterior by a pore on the left side: it is true that this pore is dorsal in *Asterina*, and lateral in *Antedon*; but then this pore has in later life a close connection with the hydrocele, with regard to which, as the diagrams show, its position is much the same in both larvæ; indeed, its position in *Antedon* is just that in which the change of position of the body-cavities would have left it, had it been originally dorsal. The position of the first rudiment of the hydrocele is also strikingly similar, though this point is not fully shown in the diagrams In both it appears on the left side, at the anterior end of the left body-cavity, in close connection with the anterior body-cavity; for, though in *Asterina* it is regarded as an offshoot of the left body-cavity, as it is in most other Echinoderms, yet it is clear from LUDWIG's description and figures that it is really formed at the junction of this cavity with the anterior body-cavity, and belongs as much to one as to the other. In *Antedon*, where the connection between these two cavities never exists, the hydrocele at first opens into the anterior body-cavity, though later it becomes temporarily shut off from it.

In both larvæ the hydrocele grows as a ring round the œsophagus, and in both again it gives off five primary radial diverticula. Two points of difference, however, strike us in the diagrams with regard to the relations of the hydrocele. In the first place, the position of the water-tube with respect to the point of closure of the water-vascular ring appears to be different; but, in the present state of our knowledge of other Echinoderms, it would be unsafe to speculate on the meaning of this difference. In the second place, in *Antedon* a radius, and in *Asterina* an interradius, is directed forwards. This may be due to the shifting of the body-cavities in *Antedon*, or be connected with the peculiar twisting undergone by *Asterina*, by which the ambulacral and anti-ambulacral systems are made to close in different interradii; but here again we touch upon the question of which part, radial or interradial, of an Echinoderm is to be considered anterior, so that this point, too, must be left for more extended investigations upon Echinoderm embryology to settle.

Returning to the diagrams, we see that there is a considerable resemblance also in the course taken by the mesentery separating the right and left body-cavities. This mesentery runs along the opposite side of the body to that which we have been examining, and is hence represented in the diagrams only by dotted lines, the alimentary canal in *Antedon* having been omitted for this purpose. Since the mesentery is incomplete in *Asterina*, no very close comparison can be made, but it will be seen that in both it runs obliquely across the anti-ambulacral side, up to the water-pore. How far this resemblance is accidental I am unable to say, but I cannot believe that it is wholly so

For a comparison of the skeleton in the two forms, so far as it can be made, I must refer to the works of previous writers (7 and 20), but I may point out that the series of interradial plates in *Asterina* developed round the right body-cavity at first forms a horseshoe-shaped curve, open towards the præoral lobe, just like the basals of *Antedon*, to which they correspond.

It might have been expected that the change in the orientation of the Crinoid larva would seriously affect the question of homologies of the plates of the Crinoidal calyx; but, as a matter of fact, owing to GOTTE's somewhat fortunate mistake, this is not the case, and P. H. CARPENTER's arguments derived from the development of the basals and orals round the right and left body-cavities respectively remain unaltered (7).

The only new piece of evidence which my observations afford on this point is the fact that at the time of its earliest development the water-pore has no connection with any of the skeletal plates; so that in this point too *Antedon* resembles other Echinoderms In fact it seems probable that this and the other external openings (mouth and anus) of the Echinoderms opened primitively in or near the median line, along which ran the mesentery separating the right and left body-cavities, and that at the time the different groups of Echinoderms separated from one another the mouth alone had departed from this position, and had taken up a definite station in the centre of the left side. The water-pore, which may have been from the first slightly on the left side, subsequently worked its way, in some groups (Crinoids and Ophiurids) on to the oral, in others (Echinids and Asterids) on to the aboral, side; so that, although its interradius probably remains the same, its position with regard to the calcareous plates is secondary. The anus, on the other hand, had already commenced to shift its position along the line of the ventral mesentery, and in some groups it continued to do so without migrating either to the dorsal or ventral side, while in others such shifting of position was soon put a stop to by the migration of the anus on to the aboral surface. Thus in the Crinoids the anus retains a primitive position, in that it still lies in the mesentery separating the right and left body-cavities (at any rate as long as this mesentery is distinguishable), while, owing to this position, it has been able to continue its shifting past the different radii to a much greater extent than in any other Echinoderms, and in this respect its position is decidedly secondary. In the Echinids and Holothurians, on the other hand, the migration of the anus to the aboral surface must have taken place comparatively early, so that in these groups it is far nearer its primitive interradius than in the Crinoids. Finally, in Asterids we have an intermediate condition, the anus having advanced further by a whole radius than in Echinids and Holothurians, but having eventually migrated towards the aboral side before reaching the interradius to which it attains in the Crinoids.

Of course, in coupling the Echinids and Holothurians together I do not mean to assert that they branched off together from the primitive Echinoderm stock. Given a primitive form, such as I have imagined, with the mouth on the left side, and the anus and water-pore lying between the ambulacral and anti-ambulacral systems, there is no reason why an aboral position for the anus should not be arrived at independently in several different groups.

How far *Antedon* exhibits a primitive feature in having its right and left body-cavities separate from the anterior body-cavity I am unable to say. Hitherto the anterior body-cavity has only been distinctly recognised in *Asterina*; but the evidence afforded by *Antedon* and *Asterina* is strongly in favour of regarding the presence of an anterior body-cavity distinct from the hydrocele as a primitive feature in Echinoderm larvæ, and it is almost certain that such a cavity will be found in other forms. The hydrocele probably opened into this anterior body-cavity from the first (its early separation in *Antedon* being probably secondary), but the water-pore appears to have belonged primarily to the body-cavity, and to have been only indirectly connected with the hydrocele.

That the completely formed free-swimming larva of *Antedon* is not primitive must be admitted, since its body-cavities have already undergone considerable changes of position; but in the possession of a distinct anterior body-cavity with a pore on the left side, followed by a pair of body-cavities which are at first lateral and approximately equal in size, it presents a closer resemblance to the larva of *Balanoglossus*, described by BATESON, in its internal anatomy than do any other Echinoderm larvæ hitherto described; and this resemblance is strengthened by its possible possession of a sense-organ at the anterior end, though, if this sense-organ is really absent in other Echinoderm larvæ, it is perhaps more probable that *Antedon* has developed it independently. In any case, the resemblance between these two larvæ, taken in connection with the well-known similarity between *Auricularia* and *Tornaria*, affords strong evidence of the common origin of the Echinodermata and Enteropneusta, already insisted upon by several writers (1, 2; 17).

SUMMARY AND CONCLUSION.

The following are a few of the more important points in the development of *Antedon* —

The mesoblast is formed from the walls of the archenteron after invagination.

The blastopore closes early at or near the posterior pole

The archenteron gives rise to four cœlomic pouches, (1) an anterior body-cavity, (2) the hydrocele, (3 and 4) the right and left body-cavities.

The hydrocele forms a ring on the ventral side of the alimentary canal, and subsequently opens by means of the water-tube into the anterior body-cavity, which communicates with the exterior by the water-pore.

The right and left body-cavities become anterior and posterior respectively, and afterwards aboral and oral. The former gives rise to the chambered organ.

After the fixation of the larva by means of the "præoral pit" the larval mouth invaginates to form the vestibule, which is rotated round to the posterior end.

The axial organ grows up from the stem in the axis of the body.

Besides the skeletal plates already known from previous descriptions, three "underbasals" are formed, which fuse with the top stem-joint. The anus opens in the same interradius as the primary water-tube (stone-canal).

In conclusion, I wish to express my most sincere thanks to my friend Dr. P. H. CARPENTER for the ready kindness with which he has assisted and advised me throughout my work.

ADDENDUM.

(Received June 20, 1888.)

While this paper was in the press an account of the development of this animal appeared by M. JULES BARROIS,* which in most points very closely resembles mine. It will probably be found a convenience that I should give a brief list of such differences as still exist between the two accounts.

(1.) BARROIS's present account (*loc. cit.*, p. 557) of the separation of the right and left body-cavities from the gut, and the subsequent fate of the latter, appears to be somewhat different from that given in his previous note (see p. 263 of this paper) But it still differs from mine in that he does not find the gut forming a complete ring round the body-cavities, but thinks that only the dorsal of the two horns of the mesenteron, seen in my fig. 6, persists. This account is certainly simpler than mine, but I consider the latter so well established by my sections that it is easier to believe that this stage (a very transitory one) has been overlooked by BARROIS.

(2.) The cavity called by me "anterior body-cavity" is for BARROIS simply the "canal du sable" (= stone-canal = water-tube). The real water-tube I believe to be a distinct structure—an outgrowth of the hydrocele—absent, or at most rudimentary, in the free-swimming larva.

(3.) In describing the ciliated bands (*loc. cit.*, p. 562), BARROIS omits all mention of the anterior incomplete one; he seems (p. 574) to have seen something of it in sections.

(4.) He still denies the prolongation of the right body-cavity into the stem, seen by GOTTE, PERRIER, and myself (see p. 268 of this paper).

(5.) On p. 280 I have alluded to PERRIER's belief that a portion of the oral body-cavity of the cystid assumes a vertical position in the axis of the body, forming the columellar cavity. BARROIS gives a similar account. To both of them that portion of the body-cavity which lies between the rectum and the parietal canal in figs. 30 and 34 of this paper is part of the oral body-cavity, while to me it is open equally to the oral and aboral cavities.

(6.) BARROIS (p. 636) attempts to show that the oral and basal plates are all developed round the right body-cavity, and he thinks that in this *Comatula* agrees with other Echinoderms (p. 634). I adhere to the old view, that the orals are formed round the left body-cavity, and the basals round the right; and shall in a future paper show that in Asterids and Ophiurids, too, some of the earliest plates to appear belong to the left side of the bilateral larva.

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* "Recherches sur le Développement de la Comatule (*C. mediterranea*)" 'Recueil Zool. Suisse,' vol. 4, part 4, April 1888, p. 546.

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EXPLANATION OF PLATES 43–47

Reference letters.

A, *B*, *C*, *D*, *E*, the different radii

Ant.	Anterior.
Dl.	Dorsal.
L.	Left.
Post.	Posterior.
R.	Right.
V.	Ventral.

All the sections are magnified about 210 diameters, unless otherwise stated. Some of the transverse sections are seen from the anterior end, others from the posterior end, but, to avoid confusion, the right and left sides are always indicated.

Figs. 45 and 46 were drawn for me by Mr. H. A. CHAPMAN.

PLATE 43.

Fig. 1. Section of gastrula, early on second day The vitelline membrane has shrunk considerably.

Fig. 2. Longitudinal vertical section of later gastrula (end of second day), showing formation of mesoblast.

Fig. 3. Longitudinal section of larva on third day, after the closure of the blastopore.

Fig. 4. Longitudinal section late on third day; the archenteron is dividing.

Figs. 5, 6, 7. From a series of longitudinal vertical sections early on the fourth day.

Fig. 5. Through the left side.

Fig. 6. Median.

Fig. 7. Through the right side.

Figs 8, 9, 10. From a series of transverse (slightly oblique) sections late on the fourth day, fig. 8 being the most anterior The mesenteron forms a ring.

Fig. 11. Transverse section early on the fifth day, at the level of the posterior end of the larval mouth. (Cp fig. 13.)

Fig. 12. Section through the same larva near the posterior end.

PLATE 44.

Fig. 13. Surface view of larva of fifth day, still in vitelline membrane; showing yellow-cells. (× 190.)

Fig. 14. Surface view of free larva, sixth day, from the right side. Yellow-cells omitted. (× 190.)

Fig. 15. Surface view, seventh day, from left side. (× 190.)

Fig. 16. Surface view, early on eighth day, just after fixing; ventral view. Yellow-cells omitted. (× 190.)

Fig. 17. Longitudinal vertical section, seventh day; median plane.

Fig. 18. Oblique longitudinal section, seventh day

Fig. 19. Part of transverse section, seventh day, about the level of the middle of the larval mouth. (× 960.)

Fig. 20. Longitudinal horizontal section near ventral side, early on the eighth day, just after fixing.

Fig. 21. Longitudinal horizontal section, seventh day, dorsal side.

Fig. 22. Longitudinal vertical section of præoral lobe, seventh day Stained with GRENACHER's hæmatoxylin. (× 460.)

Fig. 23. Longitudinal horizontal section of anterior pole. GRENACHER's hæmatoxylin. (× 460.)

Fig. 24. Transverse section through anterior part of larval mouth, seventh day. Stained with borax carmine. (× 460)

PLATE 45.

Fig. 25. Longitudinal vertical section, eighth day, a few hours after fixing.

Fig. 26. Transverse section through larval mouth, same stage as fig. 25. (× 460.)

Fig. 27. Transverse section through larval mouth, a few hours later than fig. 26. (× 460.)

Fig. 28. Longitudinal vertical section, about an hour later than fig. 27.

Fig. 29. Longitudinal vertical section of cystid, late on the eighth day.

Fig. 30. Transverse section, tenth day. (× 250.)

Fig. 31. Transverse section from same series as fig. 30, near the aboral end of the alimentary canal.

Figs. 32, 33, and 34. From a series of transverse sections, eleventh day, through the parietal canal and water-tube. (× 460.)

Fig. 35. Longitudinal section, eleventh day.

PLATE 46.

Fig. 36. Part of transverse section, tenth day, at same level as fig. 31; showing aboral mesentery and axial organ. (× 1800.)

Fig. 37. Part of transverse section from same series as fig. 36, but rather nearer the oral end. (× 1800.)

Fig. 38. Transverse section of cystid several weeks old, showing anus and water-tube (= stone-canal) in same interradius.

Fig. 39. Transverse section, near end of cystid stage, at a rather lower level than fig. 30.

Fig. 40. Part of transverse section, eleventh day, (cp. fig. 32); development of sacculus. (× 1520.)

Fig. 41. Part of transverse section through same region as fig. 40, about the twentieth day. (× 1520.)

Fig. 42. Pyriform sacs with refractive spherules from sacculi at different ages; (*a*) from cystid, about the twelfth day; (*b*) from cystid about the twentieth day; (*c*) from adult. (× 1520.)

Fig. 43. Transverse sections of two pyriform sacs from adult; deeply stained. (× 1520)

Fig. 44. Diagram of structure of adult sacculus.

Fig. 45. Diagram showing the arrangement of the skeletal plates in a larva of seventh day (cp. fig. 15). Drawn by Mr. H. A. CHAPMAN.

Fig. 46. Larva of tenth day, seen as a transparent object: the plates on the far side of the body are, for the sake of clearness, omitted (× 190.) Drawn by Mr. H. A. CHAPMAN

PLATE 47.

Fig. 47. Two plates from a larva of the seventh day; (*a*) an underbasal; this would equally well represent a basal some twenty-four hours earlier. (*b*) One of the uppermost stem-joints. (× 460.)

Fig. 48. Transverse section, tenth day, at level of the underbasals (cp. fig. 46). The dotted line shows the outline of a previous section nearer the oral pole. (× 270.)

Fig. 49. A basal plate, tenth day. (× 460.)

Fig 50. An underbasal, tenth day. (× 460.)

Fig. 51. One of the uppermost stem-joints (tenth day) with rudimentary longitudinal processes. (× 460.)

Fig. 52. Underbasals and top stem-joint fusing into a single plate, aboral view. (× 170.)

Fig. 53. Same as fig. 52, lateral view.

Fig. 54. Diagram of oral surface of adult (from Carpenter).

Fig. 55. Diagram to illustrate the probable derivation of the stage represented in fig. 3 from a gastrula with long but narrow blastopore.

Fig. 56. Diagrammatic transverse section, seventh day, to illustrate the probable connection of the chambered organ with the right body-cavity.

Fig. 57. Similar diagram, ninth day

Fig. 58 Diagrammatic view of skeletal plates (seventh day) from the posterior end. (The ventral radius should be wider).

Fig. 59. Diagrammatic view of right side of larva (seventh day), the ectoderm being removed ; showing course of mesentery.

Fig. 60. Similar diagram of left side.

Fig. 61. Similar diagram of ventral side. The mesenteron is omitted, and the course of the mesentery on the dorsal side shown by dotted lines.

Fig. 62. Similar diagram of left side of *Asterina gibbosa,* for comparison with Fig. 61. (Slightly altered from Ludwig.)

XI. *An Investigation into the Functions of the Occipital and Temporal Lobes of the Monkey's Brain.*

By SANGER BROWN, *M.D.*, *and* E. A. SCHAFER, *F.R.S.*, *Jodrell Professor of Physiology in University College, London.**

Received November 24,—Read December 15, 1887

[PLATES 48–50.]

THE experiments which we here record were performed during the preceding winter and spring in the physiological laboratory of University College, but their formal publication has been hitherto deferred because we were desirous of keeping some of the animals in which the lesions had been established under observation during several months, in order that any modification which that lapse of time might produce in the symptoms should be duly recorded. But, although not hitherto published, several of the cases, while still under such observation, have been brought before the notice of both the Physiological and the Neurological Society of London, and have been examined at different times by various persons interested in the subject of cerebral localisation, besides being familiar to the regular workers in the laboratory. In this way we have repeatedly had the opportunity of showing most of the symptoms which we are about to record, nor have we inserted any detail as to the accuracy of which there could, to an unbiased mind, be the slightest doubt.

All our experiments have been performed with the view of establishing certain lesions, uni- or bi-lateral, embracing definite areas of the cerebral cortex; and they have been confined, or nearly so, to the occipital and temporal lobes. In the performance of the operations strict antiseptic precautions were employed, the dressings being fixed by a collodion cap. On the fourth or fifth day after the operation this cap

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* I desire to acknowledge the assistance I have received, both from the Association for the Advancement of Medicine by Research and from the Government Grant Fund of the Royal Society, in aid of this series of researches. By a grant obtained from the Association many of the expenses attendant upon the procuring and keep of the animals have been met, while the Government grant has enabled me to secure the services of an able assistant (Mr. E. P. FRANCE), who has devoted a large part of his time to a careful *post-mortem* investigation of each case, with a view to the precise determination of the extent of the lesion, together with consequent degenerative changes in other parts of the central nervous system. The latter part of Mr FRANCE's work must necessarily still occupy a considerable time, and any results which it may yield will be the subject of a future communication —E. A. S.

and the dressings were removed, and in every case the wound was found to be completely closed, the edges of the skin being closely united, no sign of meningitis nor of any septic mischief being at any time perceptible. In one exceptional case, however, in which the antiseptic precautions had, from over confidence, been relaxed, the asepticism was incomplete, and sloughing of the skin over the seat of operation resulted, so that the animal had to be killed within a few days of the performance of the operation. This case will be mentioned in due course.

In a few instances, after exposing the part of the brain which was to be removed, and previous to such removal, we explored the exposed surface with the interrupted current. Since in these cases the surface of the brain had been exposed to the influence of carbolic acid, and, moreover, the animal was somewhat deeply anæsthetized, the results were somewhat uncertain, and in very many cases negative, even from parts where the experiments of previous observers would have led one to expect positive results. These incidental electrical explorations are not, therefore, of very great value, especially where their result has been negative; but such positive results as we succeeded in obtaining were duly recorded, so as to be available for future use. They will not, however, be included in the present communication.

We will now pass to the actual record of our experiments, giving them in the order in which they were performed. Afterwards we shall endeavour to point out the conclusions which seem to us to be warranted by the results which we have obtained, and to show in what particulars they agree with or differ from the results obtained by other experimenters.

I.

A small but vigorous Jew Monkey, ♂.

First Operation.—Removal of the anterior extremity (apex) of the right temporal lobe. [The *post-mortem* examination of the brain showed that the entire mesial aspect of the apex was not included in the lesion.]

Result.—Attempts were made to determine whether sapid substances were less readily detected upon one side of the mouth than the other, but without success

Second Operation.—This was performed a week after the first, the same lesion being established upon the other side of the brain.

Result.—Two days after this second operation, the animal, which was quite normal in its behaviour and appearance, and showed no signs of any motor paralysis nor any deficiency in sight, hearing, or general sensation, was tested in the following way:—Raisins and pieces of apple were given, and devoured with gusto. A raisin was then stuffed with sulphate of quinine, so that the drug was entirely concealed; this was seized and bitten eagerly as usual. But as soon as the quinine was reached the animal showed signs of dissatisfaction, smelled the raisin several times, appeared to taste it again, and finally threw it away. A piece of apple was then taken and its surface covered with the drug, which was rubbed in so as no to be recognisable by the eye After smelling the piece suspiciously, the Monkey bit off a portion with apparent confidence, but promptly rejected it. The same operation of smelling and tasting was repeated two or three times, and then the piece of apple was definitively thrown away.

This experiment was frequently repeated with a like result, although sometimes, when the animal was hungry, the food would be eaten in spite of the quinine. When, however, instead of sulphate of quinine the more soluble hydrochlorate of the alkaloid was given (especially when a little liquor strychniæ had been added) concealed in the food, the grimacing and other signs of disgust were very marked, and persisted for a considerable time.

Third Operation —The third operation was performed five weeks after the second one, and consisted in the destruction by the actual cautery of the grey matter of the superior temporal convolution of each hemisphere.

The day after this operation the animal is lively and well, and appears to hear as well as ever, so far as one can judge by his reaction to sounds. The other senses appear also to be unaffected.

On subsequent days the Monkey was repeatedly tested as to taste, sight, hearing, smell, and general sensibility, without any defect being noticeable.

A few days after the operation a patch of dry gangrene appeared on the front of the right leg, which was followed by sloughing of the skin and exposure of the muscles of the part. As the affection showed some tendency to spread, it was judged advisable to kill the animal, and this was accordingly done, by chloroform, on the fourteenth day after the third operation.

Autopsy · *Condition of the Brain* —*On the right side* (Plate 48, fig. 1*a*) there is a little softening apparent along the edge of the operculum, extending as far as the level of the lower end of the interparietal furrow, and the dura mater is somewhat adherent over this patch. The upper margin of the middle temporal gyrus is considerably damaged. The superior temporal gyrus is completely destroyed. The outer half of the anterior extremity of the temporal lobe is removed, but the inner half remains (fig. 1*b*).

On the left side (Plate 48, fig. 1*c*) there is slight adhesion of the dura on either side of the lower end of the fissure of ROLANDO. A narrow line of softening along the upper border of the middle temporal gyrus. The superior temporal gyrus is entirely destroyed, with the exception of its uppermost extremity, about 8 or 9 millims. ($\frac{1}{3}$-inch) of which is left.

The brain is shown in Plate 48, figs. 1*a* (right hemisphere), 1*b* (left hemisphere), and 1*c* (from below).

Remarks.—The results obtained in this animal appear to show that very considerable lesions of the anterior extremity of the temporal lobe may exist in a Monkey without any appreciable impairment either of smell or taste, and that the superior temporal gyrus may be completely destroyed on one side and almost completely on the other without any appreciable impairment of hearing.

II.

Rhœsus Monkey. When received, the animal was very wild and fierce, but was carefully tamed until he would readily take food from the hand. His senses, especially that of taste, were thoroughly tested. He invariably declined to eat food which was rendered bitter by quinine, expressing a lively disgust by grimacing and endeavouring to remove the impression from the mouth by his fingers.

First Operation.—The operation was bilateral, the anterior extremity of each temporal lobe being removed. This was done by vertical incision, and the *post mortem* examination showed the removal to be virtually complete.

Result.—The animal was first tested for taste on the second day, and gave no signs of any impairment of that sense Subsequently the test was frequently repeated, always with the same result. Nor could any defect in any other of the special senses be appreciated. There was no motor paralysis.

Second Operation—Three weeks after the first operation, the Monkey remaining perfectly well, a second lesion was established on the right side, the *occipital lobe* of that side being completely removed.

The day after the animal is quite well and lively, but is hemiopic Careful and repeated tests (offers of food, threats, &c.), show distinctly that there is no visual appreciation of objects on the left of the mesial plane. Objects brought across the visual field of either eye (the other being bandaged) from the left are not noticed until they reach the mesial plane

On the morning of the fifth day it was found that the animal had managed to remove the dressing and open the wound. It was therefore judged advisable, since the wound was no longer aseptic and would probably become inflamed, to kill the animal. This was accordingly done, and the brain examined.

Autopsy: Condition of Brain.—The tips of the temporal lobes are entirely removed to a longitudinal extent of about half an inch on both sides. Beyond this there is no sign of inflammation or softening. The right occipital lobe is removed except a small part of the external surface. The rest of the brain appears perfectly healthy. The angular gyrus is intact.

The brain is shown in Plate 48, figs. 2*a* and 2*b*.

Remarks.—As regards the tips of the temporal lobes, this is a more satisfactory experiment than the preceding, inasmuch as the removal is very complete, and taste and smell, nevertheless, seem in no way impaired. The result of the occipital lesion is of value merely as an *immediate* result of such an operation: it does not settle the question whether removal of this part is followed by permanent blindness, but it shows conclusively that hemiopia may be produced without any inclusion of the angular gyrus.

III.

The variety of Monkey is not recorded in the notes, ♂; very tame.

First Operation.—Destruction of the left superior temporal convolution by the galvanic cautery. No permanent symptoms resulted from this operation

Second Operation—Four months subsequently the whole of the right temporal lobe was removed by the knife.

Result—Tested the day after the operation, all the senses were somewhat deadened. On the second day, however, they have completely recovered. Hearing is quite acute, even a slight rustle, such as that caused by crushing a piece of paper in the hands, immediately attracting the animal's attention. Plugging the right ear with cotton wool did not appreciably affect the result

This Monkey continued to enjoy excellent health and to exhibit the complete possession of all his senses during a fortnight, at the end of which time a *Third Operation*—viz., the removal of the remainder of the left temporal lobe—was attempted; but unsuccessfully, for the animal did not recover from the shock of the operation.

Autopsy—On the right side the whole temporal lobe was found to have been removed or destroyed.

On the left side the removal of the lobe is also nearly complete. The superior gyrus is destroyed, and the injury even extends across the Sylvian fissure to the lower anterior end of the angular gyrus. More anteriorly, however, there is a narrow strip of the superior gyrus, about 2 millims. wide, left along the Sylvian fissure. This only includes grey matter; its white centre is completely gone

The brain is shown in Plate 48, figs. 3*a*, 3*b*, and 3*c*, and in section in figs. 3*d*, 3*e*, and 3*f*. The sections are vertical, and pass through the anterior, the middle, and the posterior parts of the lesion respectively.

Remarks.—When the left side was exposed for the third operation it was found that the destruction of the superior temporal gyrus was practically complete, if we except the small strip just mentioned, which itself showed signs of having been injured by the cautery This experiment is therefore one in which both superior temporal gyri were extensively, almost entirely, destroyed, indeed, it is scarcely possible to suppose that the very small strip which was left could carry on the function of both convolutions without any perceptible diminution. It must therefore be held to tell strongly against the entire localisation of auditory perceptions in this gyrus. The remainder of the right temporal lobe was also removed; but, as the bilateral establishment of the complete lesion was unsuccessful, no deductions can be drawn from the absence of positive symptoms following the unilateral lesion, and the experiment is of value only as a bilateral lesion of the superior gyri.

IV.

Rhæsus Monkey ; a fine specimen. Was frequently tested prior to operation.

The *Operation* consisted in the complete removal of the whole of the right temporal lobe, down to the edge of the crus cerebri, and including the hippocampus major. Behind, the lesion extended partly over the under surface of the occipital lobe

Result.—Two days after the operation the following notes were taken .—There is distinct facial paralysis (left side) There is also right hemianopsia. Reactions to tactile impressions applied to the left side of the body are much diminished When pricked with a needle upon the left side, scratches the spot pricked, but does not show evidence of feeling pain from the prick. On the right side, on the other hand, there is prompt reaction both to tactile and painful impressions

On the eighth day the reaction to touch and to pricking is nearly, if not quite, equal on the two sides, but the facial paralysis and hemiopia persist.

On the seventeenth day the animal had to be killed, because the skin wound had become re-opened, and there was evidence of the commencement of inflammation and hernia cerebri.

Autopsy.—The right temporo-sphenoidal lobe was found to be completely destroyed , the commencing hernia had produced a slight prominence of the brain over the seat of lesion. The upper part of the right occipital lobe is slightly yellowish, as if from commencing softening.

The brain is represented in Plate 49, fig 4*a*, from the side, and in fig 4*b* from below.

Remarks —The lesion not being bilateral, experiments upon hearing, smell, and taste could not be satisfactorily carried out. The hemiopia was probably due to a large portion of the occipital lobe having accidentally become involved, at least in its vascular supply; the facial paralysis to obliteration of vessels proceeding to the "facial area" from the Sylvian fissure. The affection of general and tactile sensibility may be due to the fact that the hippocampal region was involved in the removal.

This case furnishes an illustration of the fact that hernia cerebri is apt to accompany the establishment of a septic condition in the exposed brain.

V.

A small but vigorous and intelligent *Rhæsus* Monkey, ♀.

First Operation.—The left angular gyrus was destroyed by actual cautery.

The result of this operation was absolutely *nil*, so far as we were able to determine. Even an hour or two after the establishment of the lesion and recovery from the effects of the anæsthetic, no impairment of vision could be detected. On bandaging the left eye the animal still saw perfectly well with the other one, took food from the hand, avoided obstacles, and generally displayed every token of the possession of clear visual perceptions. There was no loss of movement of the eyeball or eyelid, nor any anæsthesia of the cornea.

Second Operation.—Was performed eight days after the first, and consisted in the destruction of the remaining angular gyrus in the same manner.

Tested in less than an hour after the operation, shows no impairment of vision, nor of the motion of the eyeballs or lids, nor was the cornea of either eye rendered anæsthetic, or even, so far as could be determined, diminished in sensibility The animal was kept for a month without further operation, during which time it was frequently tested, but always with negative results.

Third Operation.—A month after the last. This operation was intended to effect the destruction of the superior temporal gyri on both sides, the greater part being cut away with the knife, and the destruction of the remainder right up to the bounding fissures being completed by the actual cautery. It was found, however, on *post-mortem* examination, that on the right side the second temporal gyrus had been mistaken for the first, and that the latter had remained almost intact. This mistake was not suspected during life, and the animal was always shown as one with both superior temporal gyri destroyed.

Results.—The only noticeable symptom in this animal is an apparent stiffness of the neck, so that when she desires to rotate the head, the shoulders and upper part of the trunk move also. This appears to produce a certain amount of reluctance to turn towards sounds and objects which might attract the attention, and a consequent appearance of stupidity; but she nevertheless gives unmistakable signs that she hears acutely, and also that she is able to localise the direction of sounds. No other symptoms but the one mentioned—the appearance, namely, of stiffness of the neck—could be detected in this animal, although she was under daily observation for some months, and was frequently carefully tested with respect to all the special senses.

About four months after the first operation, having been in very fair health during that time, the animal was seized with epileptiform convulsions, which continued without intermission for a number of hours and only ended with death.

Autopsy · *Condition of the Brain*.—The superficial grey matter of both angular gyri is destroyed. The lesion also involves the posterior border of the external parieto-occipital fissure. On the left side the superior temporal gyrus is destroyed. On the right side this convolution remains, but the second temporal gyrus and the portion of the temporal lobe immediately below it are destroyed. The rest of the brain is healthy, with the exception of a small patch of yellow softening in the middle of the left ascending parietal gyrus.

The brain is represented in Plate 49, figs. 5*a*, 5*b*, and 5*c*.

Remarks.—This experiment is of especial interest, firstly on account of the totally negative results, both immediate and remote, of decorticization of the angular gyri; secondly, by reason of the peculiar stiffness and immobility of the neck which followed the second operation; and thirdly, because it is the only one of our experiments upon the upper part of the temporal lobe as to the result of which any decided doubt was expressed by outside observers to whom the animals were from time to time exhibited. The doubt expressed was as to the possession of the auditory faculties, and probably arose from the peculiar stiffness and reluctance to turn the head which has been recorded. We ourselves, and all who have had much to do with the Monkeys, obtained on so many occasions abundant evidence of acuteness of hearing that we never shared the doubt in the slightest degree, although we performed the operation in the hope and expectation that hearing would be decidedly affected or totally destroyed. For our previous experiments had shown that both superior temporal gyri could be destroyed without loss of hearing; we thought it possible, however, that if this lesion were combined with the destruction of the angular gyri a positive result might be obtained. In other words, we were desirous of testing the question whether the centre for auditory impressions were localised in these two gyri (the angular and superior temporal), which are anatomically almost continuous with one another, and which we thought might also have a physiological connexion. But our expectations were disappointed, as we had no difficulty in observing, and as we also had no difficulty in convincing most other observers Of course, it must be borne in mind, what we were at the time of testing in ignorance of, that the lesion was not that which we supposed it to be, since only one of the superior temporal gyri was involved in it.

VI.

A fine, large, active *Rhæsus* Monkey, ♂.

First Operation.—Complete removal of the right temporal lobe.

Result.—Immediately after recovery from chloroform it was observed that he had left hemiopia. Little, if any, difference of sensibility could be detected on the two sides of the body, nor any muscular paresis. The following day there was still evidence of hemiopia, but it did not persist for more than a day or two.

Second Operation.—Five days after the first operation, the wound of which had completely healed, and the animal being in good health and spirits, the remaining (left) temporal lobe was cut away. In both cases the removal was very complete, as was shown on *post-mortem* examination.

Results.—These severe operations were recovered from with marvellous rapidity, the animal appearing perfectly well even so early as the day after the establishment of the second lesion. A remarkable change is, however, manifested in the disposition of the Monkey. Prior to the operations he was very wild and even fierce, assaulting any person who teased or tried to handle him. Now he voluntarily approaches all persons indifferently, allows himself to be handled, or even to be teased or slapped, without making any attempt at retaliation or endeavouring to escape. His memory and intelligence seem deficient. He gives evidence of hearing, seeing, and of the possession of his senses generally, but it is clear that he no longer clearly understands the meaning of the sounds, sights, and other impressions that reach him. Every object with which he comes in contact, even those with which he was previously most familiar, appears strange and is investigated with curiosity. Everything he endeavours to feel, taste, and smell, and to carefully examine from every point of view This is the case not only with inanimate objects, but also with persons and with his fellow Monkeys. And even after having examined an object in this way with the utmost care and deliberation, he will, on again coming across the same object accidentally even a few minutes afterwards, go through exactly the same process, as if he had entirely forgotten his previous experiments. His food is devoured greedily, the head being dipped into the dish, instead of the food being conveyed to the mouth by the hands in the way usual with Monkeys He appears no longer to discriminate between the different kinds of food; *e.g*, he no longer picks out the currants from a dish of food, but devours everything just as it happens to come. He still, however, possesses the sense of taste, for when given a raisin which has been partly filled with quinine he shows evident signs of distaste, and refuses to eat the fruit.

It is also clear that he still both sees and hears. The field of vision appeared at first somewhat limited, and he also seemed to see somewhat indistinctly, making, for example, one or two unsuccessful attempts to pick up a currant from the floor before finally succeeding. This condition, however, soon passed off. He reacts to all kinds of noises, even slight ones, such as the rustling of a piece of paper, but shows no consequent evidence of alarm or agitation, although his attention is evidently attracted by sounds. Thus he was observed to follow with his head the sound of footsteps passing along the corridor just outside his room, directing his attention to them as long as one could oneself distinctly hear them.

This peculiar mental condition was observed for some weeks, becoming gradually less noticeable. A week after the second operation it is noted that he appears brighter in disposition, and is again commencing to display signs of tyrannising proclivities towards his mate, for which he had been remarkable previously. About this time a strange Monkey, wild and savage, was put into the common cage. Our Monkey immediately began to investigate the new comer in the way described, but his attentions were repulsed, and a fight resulted, in which he was being considerably worsted. The animals were, however, separated and tied up away from one another, but our Monkey soon managed to free himself, and at once proceeded, without any signs of fear or suspicion, again to investigate the stranger, having apparently already entirely forgotten the result of his former investigation.

Two weeks after the second operation it is noted that this Monkey continues to "investigate" objects, but with diminishing frequency and thoroughness. He is either rapidly regaining some of his former experience and memory, or forming altogether new ones. He now takes his food up with his hands, and also pays a more natural attention to his fellows than before. All his senses are acute.

Five weeks after the operation his curiosity has sensibly diminished, and he is slowly regaining his former mercurial temperament, continuing, however, tame.

This Monkey was kept for nearly eight months after the operation Long before the expiration of that time he had regained full possession of his mental faculties, and became one of the brightest and most intelligent animals that we had experience of, domineering over all the other Monkeys which were kept in the same cage with him. He was shown to and tested before the Physiological and Neurological Societies, and was also seen privately by several eminent neurologists. With regard to this Monkey there was no difference of opinion expressed, but it was universally admitted that all his senses, including that of hearing, were perfectly acute Indeed, it was eventually impossible to detect any abnormality of the cerebral functions.

The animal eventually died of dysentery, after a short illness

Autopsy —With the exception of the large intestine, which is ulcerated and inflamed, all the organs appear healthy. In the brain the whole of the temporal lobe is completely removed upon both sides; the lesion extending quite up to the Sylvian fissure on the outer surface, and reaching to the inner edge of the hemisphere on the under surface. On the right side the lesion does not quite reach the parieto-occipital fissure on the external surface, but on the left side the removal extends quite up to this fissure. A very small piece of the antero-inferior edge of the lobe remains on the left side, but this is undermined and cut off from the medullary centre. No trace of the superior temporal gyrus is left on either side, except a part of the grey matter bounding the Sylvian fissure below, and this grey matter is devoid of its corresponding medullary centre. The brain is shown from each side and from below in Plate 49, figs 6*a*, 6*b*, 6*c*, and in vertical sections through the anterior, middle, and posterior parts of the lesion in figs. 6*d*, 6*e*, and 6*f*.

Remarks.—This is the most extensive bilateral lesion of the whole temporal region which we have performed. What is most remarkable about it is the *immediate loss* and *ultimate recovery* of the intellectual faculty. On localisation of functions the experiment throws no direct light; what evidence there is being entirely negative. The general bearings of its results will be referred to later on

VII.

Bonnet Monkey of medium size, ♂.

First Operation.[*]—A piece of the skull having been removed near the vertex, the right half of the brain was gently drawn aside, and the middle part of the gyrus fornicatus was scooped away. In spite of the greatest care being taken, the marginal convolution suffered a little injury in the attempt to get at the subjacent gyrus fornicatus.

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[*] The first and second operations were performed by me, before the commencement of our joint investigation.—E. A S.

Result.—The immediate result of the operation is to produce anæsthesia, partial in some parts, complete in others, over the whole left side of the body. The left arm, from the elbow downwards, retains, however, its sensibility. The rest of the arm, the trunk, and the leg have very little, if any, sensibility, for the most part there is no reaction either to a touch or the prick of a pin, but sometimes the latter produces a slight movement, unaccompanied however by the general wincing which is produced by a prick on the right side of the body. The leg is slightly, but perceptibly, paresed. This condition continued, with a very slight and gradual improvement, for about seven weeks, when a second operation was undertaken

Second Operation—This consisted in the resection of the whole of the right temporal lobe, including the hippocampal region and the hippocampus.

Result—No noticeable effect followed the second operation The previous anæsthesia was maintained, but not perceptibly increased, and, although the gradual improvement before alluded to continued to progress, a difference of sensibility upon the two sides of the body (except in the arm, below the elbow) was still manifest eight months after the first operation. It was now decided to establish a lesion upon the opposite side of the brain

Third Operation—The left superior temporal gyrus was exposed, and after being tested by faradic excitation its grey matter was extensively destroyed by actual cautery.

Results.—The results of this third operation were practically *nil.* The animal suffered from some epileptiform attacks on the day after the operation, but had recovered on the third day, and showed no difference from his previous condition. Hearing tested, and found to be very acute.

Fourth Operation—It was next determined to explore the right side of the brain, and to destroy completely any part of the right superior temporal gyrus that might perchance have been left from the second operation This was accordingly done five days after the third operation. On reflecting the skin and membranes it was found that the superior gyrus had been very completely removed, except 1 or 2 millims. of the superior and posterior extremity. This produced no reaction on being faradized, and might be concluded to have lost its functions. The actual cautery was however applied to it and to the anterior inferior extremity of the lobe, a little of which was also left.

Result.—Three hours after the production of this fourth lesion, the Monkey having recovered from the immediate effect of the operation and of the anæsthetic employed, his hearing was again tested and still found to be very acute, his attention being immediately directed even to small noises such as a kissing or sucking noise made with the lips, clinking of coins, or the rustling of paper.

Subsequent testing at intervals during the next few days having revealed no further symptoms, the Monkey was killed twelve days after the last operation.

Autopsy.—On the right side of the brain the middle part of the gyrus fornicatus has disappeared, and the corresponding part of the marginal gyrus is somewhat depressed and injured. Almost the whole of the temporal lobe is removed A narrow strip on the under surface of the occipital lobe has undergone softening and disintegration. On the left side the superior temporal gyrus is destroyed, except its lower (anterior) extremity (tip of the lobe). The surface of the brain just above and in front of the Sylvian fissure has been slightly injured. The brain is shown in Plate 50, figs. 7*a*, 7*b*, and 7*c*.

Remarks.—The first two operations, viz, on the gyrus fornicatus and on the temporal lobe and hippocampal region of the right side, may be looked upon as a continuation of the experiments upon the limbic lobe which have already been published,* and of which they form a complete corroboration But none of those cases were kept alive with continuation of the symptoms for so long a period as this one

Otherwise, the Monkey affords another instance of an extensive bilateral lesion of the superior temporal gyrus with complete retention of auditory perceptions.

VIII

A fair sized but rather ill-nourished Jew Monkey, ♂.

Operation.—Complete resection of the left occipital lobe. The operation was performed under chloroform alone (without the morphia which we have often given in addition) and was quite clean and bloodless.

Result.—The sight was tested about an hour after the establishment of the lesion, and it was found that there was complete right hemiopia, no objects on the right side of the mesial visual plane being seen, although on passing them across the mesial plane they are at once observed.

The next day and repeatedly after that the test was applied, and always with the same result. When each eye was successively covered with adhesive plaster the right half of the retina of the uncovered eye was still found to receive and convey visual impressions to the sensorium, but the images of objects falling upon the left half of the retina produced no impression. The exact boundary of the hemiopia could not be determined, but the above is true as a general statement

There was no loss of sensibility of the cornea of the opposite eye, nor any paresis of the ocular muscles.

The animal was kept for eight months without any sign of recovery from the hemiopia. It was repeatedly shown both to occasional visitors interested in cerebral physiology and also to the Neurological Society. There was never any difficulty in exhibiting its defect. Although greedily fond of raisins, the animal could never see or seize one until it had been brought so that its image fell upon the right half of one or both retinas. There was no attempt to avoid a threatened blow, aimed from the right side, although when such a threat was made from the other side the animal invariably winced and endeavoured to evade it. When placed on a floor strewn with currants the Monkey invariably picked up only those which lay on the left side of his mesial visual plane, and this caused him to be turning constantly round towards the left as the nearer ones were exhausted. Moreover he was apt, when driven, to knock against obstacles which lay on the right-hand side of his course. Finally, about eight months after the operation, it was determined to kill the animal and examine the brain. This determination was arrived at partly on account of the fact that the animal had for some few weeks been losing flesh, and it was feared that he might not in any case survive much longer. But, prior to carrying out the decision, it was thought advisable to examine the eyes carefully with the ophthalmoscope, and for this purpose we obtained the experienced co-operation of Mr. J. TWEEDY, the Professor of Ophthalmic Surgery in University College. Apart, however, from a general pallor, due probably to anæmia, there was little definite change. "The inner half of the right disc is, perhaps, a little paler than the corresponding half of the left, but compared with those of healthy Monkeys both discs are decidedly pale, with very little of the pink stippling characteristic of healthy nerve"

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* HORSLEY and SCHÄFER, 'Phil. Trans.,' B, 1888.

Autopsy—The cause of the wasting and anæmia seems to be the presence of numerous worm-like parasites in the lungs. The left occipital lobe is exactly and entirely removed. All the rest of the brain appears perfectly healthy, even the angular gyrus and the other parts next the occipital lobe being quite intact. The cut surface looks as if the incision and removal had been made at the autopsy instead of during life and eight months previously. The appearance of the brain from above is represented in Plate 50, fig 8.

Remarks.—This is in every way a definite and satisfactory experiment. The lesion is limited to the one occipital lobe, the whole of which is involved. The resulting hemiopia is well-marked and persistent

IX.

Small Jew Monkey, ♂.

Operation.—Bilateral resection of the occipital lobes.

Result.—Complete and permanent blindness. The eyes at first have a protruding staring appearance, but this is not persistent, and after a few days they appear normal. This animal does not seem to see any objects, however large. When released runs against all obstacles in his path, but after a time learns to grope his way about the room. Can only find his food by groping for it. Although very wild and timid, makes no attempt to evade a threatened blow, but when touched even in the lightest manner flies away displaying great alarm. If a raisin is dropped near him gropes about for it, but cannot see it even if placed on a sheet of white paper. Hearing and other senses appear very acute The corneæ retain their full measure of sensibility, and there is no paresis of any of the ocular muscles. Although absolutely unable to see ordinary objects or to form any appreciation regarding them by aid of the visual sense, it is not quite easy to decide whether he is able to distinguish between light and darkness, for, when a large object such as a tray is held between him and the light, he will sometimes put up his hand as if to touch it He does not, however, always respond in this way, and it is possible that the object may be appreciated by other senses than that of sight; for when a strong light is suddenly flashed upon him his attention is not diverted towards it. The animal was examined ophthalmoscopically by Mr Tweedy eight months after the operation, who reports nothing abnormal with the exception of a "slight effusion along the perivascular sheaths, possibly indicative of increase of the subarachnoid fluid."

This animal was kept in good general health, and with no apparent abatement of the blindness, for more than nine months. Before killing him for the purpose of examining the condition of the brain it was determined to test him as thoroughly as possible, so as to decide whether there was any discrimination between light and darkness For this purpose he was placed in a dark room, and through a hole in a shutter a beam of direct sunlight was admitted, and intermittently flashed upon his eyes from a mirror. Whether the flashes were allowed to follow one another rapidly or slowly, or whether the light were kept directed straight into his pupils, the result upon the behaviour of the animal was absolutely *nil* Other Monkeys under like circumstances directed their attention towards the mirror when the light was alternately flashed upon them and immediately removed; and when it was kept directed towards them avoided the glare. The conclusion appears therefore unavoidable that, so far as the perceptive faculties are concerned, this animal was totally blind. It is scarcely necessary to say that the pupils reacted to light in a normal manner. The movements of the eyeballs also seemed to be quite natural, so that, although the animal exhibited a somewhat characteristic vacant stare, the blindness could not have been guessed at merely from the appearance of the eyes

Autopsy. Condition of the Brain.—Both occipital lobes are exactly and completely removed. The angular gyri, which are very well developed in this Monkey, are intact, except that a little of the grey matter in the depth of the external parieto-occipital fissure is cut off. The lesion extends below a short distance forwards on to the under surface of the temporal lobe in both hemispheres. There is no sign of any old inflammatory condition either of these or of any other portions of the cortex.

The brain is represented in Plate 50, fig. 9.

X.

Small Jew Monkey, ♂.

Operation.—Resection of both occipital lobes.

Result.—The blindness is not so complete in this case as in the last. Even the day after the operation he appears to have a dim perception of objects held between his eyes and the light Cannot, however, find a raisin placed on a sheet of white paper, and gropes about much in the same way as the other. There is no diminution of sensibility in the corneæ, nor any paresis of the ocular muscles.

This animal was kept alive for several months, and the permanent effects of the operation, which persisted during the whole of that time, were as follows:—

There is no visual perception for objects which lie below the horizontal plane through both visual axes Above this plane there is some visual perception, but it is very indistinct. It is more distinct for things above and on the right side than elsewhere. Objects, such as raisins, strewn upon the floor are only found by groping. A threatened blow aimed from below is not noticed, but from above or from either side and above it is winced at

This Monkey remained in apparently good health for about eight months, being eventually killed for the purpose of examining the brain.

Autopsy Condition of the Brain.—The occipital lobes are entirely removed (fig. 10*a*) with the exception of a small portion of the external surface of the right lobe, which persists to the extent shown in fig. 10*b*, Plate 50. The lesion involves a little of the under surface of the temporal lobe, but less than in Monkey No. 9. The angular gyri are intact, and all the rest of the brain appears perfectly normal.

Remarks.—It is noteworthy that in this animal, as compared with the last, a very small portion of one occipital lobe was left, and that the retention of this small portion of the external border of the lobe was accompanied by retention or re-acquisition of visual perceptions for objects falling upon a certain limited part of the retinæ.* The significance of this fact will be afterwards alluded to.

XI.

Small Jew Monkey, somewhat weakly, ♂

Operation —Bilateral destruction of the superior temporal gyrus.

Result.—On testing the hearing it is found that the animal reacts even to small noises, invariably looking up when paper is crumpled near him. This Monkey suffered considerably from shock, and for the day or two after the operation remained in a stupid lethargic condition, refusing food. He began to rally on the third day, and to give distinct attention to slight sounds, such as the snapping of the fingers near his head. On removing the dressing it was found that the skin had not completely united, but it was re-dressed, and a dose of morphia was given to quiet the animal and prevent his attempting the removal of the dressing. The morphia, however, proved fatal, the effect of shock having probably been increased by the administration of that drug

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* Compare MUNK, *op cit.*, p 39.

Autopsy.—Both superior temporal gyri are completely removed.

There is no sign of extension of inflammation, the rest of the brain appearing perfectly healthy.

The brain is shown in Plate 50, figs. 11*a* and 11*b*.

Remarks.—This experiment, although not successful so far as the prolonged maintenance of life after the production of the central lesion was concerned, is complete so far as relates to the supposed exclusive relation of the superior temporal gyri to the auditory functions, for there was no question of a doubt that the attention of the animal was roused even by slight noises after the entire destruction of both those convolutions.

XII.

Large vigorous *Rhæsus* Monkey, ♀.

First Operation —The left superior temporal convolution was completely scooped out, so that not only was the grey matter on the outer surface removed, but also that in the Sylvian and parallel fissures and the white matter of the convolution.

Result.—The animal rapidly recovered from this operation without any appreciable symptom.

Second Operation.—On the tenth day after the first operation the right superior temporal gyrus was removed in the same manner and as completely as the left had been.

Result —As soon as the animal was recovered from the effect of the anæsthetic her hearing was tested, and, although still somewhat lethargic, she was found to give attention even to slight sounds, such as kissing or sucking noises made with the lips This was repeatedly tried, and she invariably responded by looking up

This Monkey made a rapid recovery; indeed the double operation produced no perceptible effect upon its general health. But the creature shows the same change of disposition that was manifest in Monkey No. 6. She appears to have lost, in great measure, intelligence and memory. She investigates all objects, even the most familiar, as if they were entirely unknown, tasting, smelling, and feeling all over everything she comes across. She is tame, and exhibits no fear of mankind, but shows uncontrollable passion on the approach of other Monkeys, so that it is now necessary to shut her up in a cage by herself. Like Monkey No. 6, she now invariably devours her food by putting her head down to the platter, instead of employing the hands to convey it to her mouth. Moreover, her appetite is insatiable, and she crams until her cheek-pouches can hold no more. She evidently still sees, hears, tastes, and smells perfectly well, but her understanding of the impressions which she derives from her senses is unquestionably small. Cutaneous sensibility shows no appreciable diminution.

The peculiar idiotic condition into which this Monkey was thrown by the operation was more persistent than in the case of No. 6. Recovery proceeded but gradually;

and, although in many points improvement was manifest, there was never, during the whole time that the animal was kept, that complete return of intelligence which was observed in No. 6 (which had, it will be remembered, a much more extensive bilateral lesion). Her appearance remains stupid, and her movements lethargic; she is still savage towards her fellow Monkeys; her attention is not easily attracted, either by sights or sounds, although an abrupt movement or a sudden and unusual noise will produce signs of perception. She usually takes her food up with her hands, but is still markedly greedy, taking, when she can get it, much more food than a normal Monkey of the same size

After being kept under observation for more than eight months, during which she was exhibited to numerous visitors and to the Neurological Society, the animal was killed and the brain examined.

Autopsy.—Both superior temporal gyri are completely removed, and their place is occupied by a large fissure in which the island of REIL can be seen. The rest of the brain is, to all appearance, normal.

The brain is shown in Plate 50, figs. 12*a* and 12*b*.

Remarks —What is most remarkable in this case is the fact that a comparatively limited bilateral lesion of the cerebral surface should have produced so considerable a change in the general cerebral functions The case of Monkey No. 6 is far less striking in this particular, because the bilateral lesion *there* was very extensive; moreover, the loss of intelligence was far less persistent, although at first not less distinct.

The experiment is quite conclusive against the localisation of auditory perceptions in the superior temporal gyri alone. In this case there was certainly no trace remaining of either convolution, and the animal could unquestionably hear, even slight sounds. Whether the appreciation and discrimination of sounds remained the same is a point which, it must be admitted, it is hardly possible to solve satisfactorily by experiments on animals. But in this case, at least, even if it had been possible (which it was not) to prove that the discrimination of different sounds was abolished or diminished after the lesion, such abolition or diminution must still be looked upon merely as one of the manifestations of the general idiocy which was produced by the operation rather than as due to the interference with any special auditory function of the part.*

XIII.

Vigorous *Rhæsus*, ♂.

Operation.—The whole of the left angular gyrus, to a depth of 6–7 millims., was scooped away, the removal being completed up to and including the grey matter in the fissures bounding the convolution.

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* The extensive character of the lesion of the superior temporal gyrus in this case, and also in that of Monkey No. 6, having been called in question by Dr. FERRIER (*Vide* Article in 'Brain,' April, 1888), I have caused photographs of these two brains, and of sections across them, to be made, and intend to publish these photographs in the succeeding number of 'Brain.'—[E. A. S., June 18, 1888].

Result.—The immediate effect of the operation was to produce hemiopia, the left side of both retinæ being apparently blind. This condition lasted for a few days, but gradually passed off, so that no visual disturbance could after a time be detected. The animal is still alive and well (November, 1887), eight months after the operation. There has never been any deficiency of sensibility in either eyeball, nor any paresis of the muscles moving either the eyeball or the eyelid.

General Remarks.

With the exception of one experiment upon the gyrus fornicatus, the results which we have here recorded bear entirely upon the functions of the temporal and occipital lobes and of the angular gyrus, and our object in undertaking them was to decide, if possible, between the conflicting results of preceding experimental observers, and especially those of FERRIER, MUNK, and LUCIANI and TAMBURINI.

In the first edition of his elaborate work on the 'Functions of the Brain,' published in 1876, FERRIER gave a clear and succinct statement of his views upon the functions of these parts, based for the most part on experimental investigations, carried out chiefly upon Monkeys, which had been published by him *in extenso* in the 'Philosophical Transactions.' To the views there enunciated we need not, however, specially refer, because they have been in some measure modified and superseded by the author's more recent utterances in the second edition of the book, which was published only last year, and have therefore come to possess merely a historical interest in connexion with the development of the general question of localisation of functions in the brain Between the appearance of the first and second editions, Dr FERRIER undertook, in conjunction with Professor G. YEO, a renewed investigation into the functions of these and other parts of the Monkey's brain; and their results, which are given in full in the 'Philosophical Transactions' for 1885, are embodied in the later edition. We may take it, then, that the mature judgment of the author is set forth in the second edition; and it is with the views which we there find that we propose to deal.

The experiments of MUNK, mainly on Dogs but also on Monkeys, have been published from time to time in the 'Verhandlungen der Berliner Physiologischen Gesellschaft'; and these papers have been collected by the author, and re-issued in a separate form.* It is to this collection that we shall chiefly refer in alluding to MUNK'S views regarding the functions of the parts we have been dealing with

The results obtained by LUCIANI and TAMBURINI are detailed in two communications, "Sulle Funzioni del Cervello," 1878 and 1879, of which excellent critical digests are given in 'Brain,' vols. 1 and 2; whilst the results of later experiments by LUCIANI alone are given by himself in a more recent number of the same periodical ('Brain,' vol. 7, "On Sensorial Localizations in the Cortex Cerebri").

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* H. MUNK, 'Gesammelte Mittheilungen aus den Jahren 1877-80' Berlin, 1881

We will consider first of all our experiments upon the occipital lobe, because the results yielded by them are definite and positive, whereas our results regarding the other parts which are the subject of this paper have been mainly negative.

We record three experiments upon the occipital lobe,* one being unilateral and the other two bilateral. In the unilateral case, and in one of the bilateral, the lesion was practically confined to that lobe, and at all events did not involve the angular gyrus. In the third case the grey matter of that gyrus in the depth of the parieto-occipital fissure is slightly injured. In all three the superficial lesion extends a short distance on to the under surface of the temporal lobe. In the unilateral operation (Case No. 8), in which only one of the occipital lobes was removed, the operation was followed by immediate and persistent blindness for all images falling upon the corresponding half of each retina (bilateral homonymous hemianopsia). In one of the bilateral operations (Case No. 9) the establishment of the lesion was followed by complete and persistent blindness of both eyes. In the other bilateral operation (Case No. 10) the blindness which was produced, although quite persistent, was not so complete as in the other; but images which fell upon the lower part of the retinæ were still capable of producing impressions, whether distinct or not it is impossible to say, which were transmitted to, and perceived by, the brain. In this case, however, it was found that a very small part of the occipital lobe had escaped removal, so that it does not fall, like the other two, into the category of experiments in which the whole lobe of one or both sides was entirely removed.

The two experiments in which the ablation respectively of one and both occipital lobes was complete are entirely confirmatory of the statements of MUNK on this point, who asserts that complete and permanent blindness is produced by removal of the occipital lobes alone, without the implication of the angular gyri,† and that removal of one occipital lobe causes complete and permanent hemianopsia. LUCIANI obtained the same *immediate* result, but the blindness was not persistent; moreover, he states that the result is not confined to lesions of this lobe, although better marked and more persistent when it is included in the lesion. HORSLEY and SCHÄFER‡ also obtained either entire blindness or hemianopsia, according as the operation upon the occipital lobe was bilateral or unilateral, only as a *transitory* condition; but in the cases they have described the result of *post-mortem* examination showed that the removal of the occipital lobes was never quite complete. In one case in which, after an incomplete destruction of both occipital lobes, which had been followed by the usual result obtained in such cases—viz., at first total blindness, followed after a few days by a considerable amount of recovery—subsequent destruction of the angular gyrus of one side caused hemianopsia which appeared permanent. But there is reason to believe that the permanent blindness in this case was due, not to the lesion of the angular gyrus, but to the fact that, in removing this convolution, a part of the occipital lobe which had been left from the first operation was also removed. The temporary complete blindness which often follows even incomplete ablations of the occipital lobe is easily understood, if we remember that the immediate effect of such ablations may extend to the parts of the lobe which are not actually involved in the removal—a temporary disturbance of their function being produced by the interference with the circulation in the adjoining parts, owing to the occlusion of the blood-vessels of the ablated portion, and also by the removal of the support which they naturally obtained from that part whilst still *in situ*. These conditions of disturbance soon remedy themselves, but while they last they must affect the functions of the parts which are thus disturbed.

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* Really four, but one (Case No. 2) need not be referred to here, since the animal was not kept long enough to judge of the persistence of the hemiopia produced.

† MUNK remarks (p. 39), "After a time, and very gradually, the sight somewhat improves;" but the only evidence of this appears to be that the animal can move about slowly without knocking against obstacles.

‡ *Op. cit.*

Our present results are at variance with those of FERRIER, who denies that the removal of the occipital lobes alone is followed by any, even temporary, deficiency of vision. We may remark, however, that in the cases of which figures are published by FERRIER, either of his own experiments or of those which he performed in conjunction with Professor YEO, the occipital lobe is in none shown to be completely removed; on the contrary, in some little more than the cauterisation of the external surface has been attempted, and in all the others considerable portions of the lobe are left. This amount of lesion might very well be accompanied by the retention of so much visual perception that it might be difficult or impossible to recognise in animals any functional defect. This, at least, is the only way in which we can reconcile the discrepancies between the results of FERRIER and YEO, on the one hand, and those of MUNK, of LUCIANI and TAMBURINI, of HORSLEY and SCHAFER, and of ourselves, on the other hand. These two experiments, viz., those in which the occipital lobe was totally removed, (1) unilaterally, and (2) bilaterally, appear to afford a complete demonstration of the idea that in the cerebral perception of visual impressions that lobe, and that lobe only, of the cerebral hemisphere of the Monkey is concerned. They must, of course (to arrive at the whole of this conclusion), be taken in conjunction with other experiments in which uni- or bi-lateral lesions have been established by ourselves and by previous investigators in other parts of the cortex. Certainly in our hands, and in the very numerous experiments of HORSLEY and SCHAFER, we have not found in any single instance in which the occipital lobe has not been involved in such lesions any but the most transient influence exerted upon the visual functions (except in those cases like our Nos. 6 and 11, in which, from the situation or extent of the injury, a general depression of the cerebral functions has resulted, and a condition resembling idiocy has been established).

We have made one or two experiments with the view of testing the assertions of MUNK regarding the connexion of the several parts of the visual receptive surface—the retina—with parts of the visual perceptive surface—the cortex of the occipital lobe. But the localised lesions which we have produced, after the more extended disturbance which is temporarily caused by the operation has subsided, have not so far yielded any permanent results that we could in these animals appreciate. We have not found it possible to determine, as MUNK would appear to have done,* the existence of localised central blindness. Indeed, the difficulty of such determination in these animals seems to us to be well nigh insuperable. On account of this difficulty and the necessary incompleteness of those experiments we have not recorded them in this paper, and do not for the present propose to do so. But the third experiment upon this region which we have recorded does certainly favour the idea of such a connexion or projection. In this, a very small part it is true, but still a part, of the occipital lobe of one side remained intact, and the animal, in place of being completely blind, like that in which every trace of the lobe has been removed, retained its visual perceptions, probably imperfect ones, for impressions affecting a part, and a part only, of both retinæ. This is the only case in which we were able to substantiate what, for want of a better term, we will speak of as co-related localisation in the occipital lobe; but although it stands singly, it is both positive and well-marked, and affords, therefore, important evidence of the existence of such co-relation in a sensory area.

We will next consider the results which we have obtained from destruction of the angular gyrus. This convolution has attracted a great amount of attention from others as well as ourselves, because it is the part of the brain which was originally believed by FERRIER to be exclusively concerned with the appreciation of visual impressions derived from the opposite eye; and, although this position is somewhat modified in the later edition of his book, it is still regarded as a most important part of the cerebral visual centre, viz., as connected with the appreciation of those visual impressions which affect the yellow spot or centre of direct vision. When examined into, it will, however, be found that this opinion rests mainly upon the fact that a very temporary visual disturbance may follow its destruction or injury Certainly we have ourselves in one or two cases obtained this result, nor is it to be wondered at if we accept the conclusion that the adjacent occipital lobe is the real cerebral visual centre.

For the effect of operating upon the angular gyrus may, and sometimes does, produce such a temporary disturbance in the adjoining occipital lobe as to depress the functions of this, or even temporarily to abolish them. The same result is often got by operating on the temporal lobe. But the symptoms are not permanent and may even be altogether absent, and the result of operating upon this gyrus offers indeed a very striking contrast to the result of removing the lobe behind it.

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* At least in Dogs.

MUNK* denies the participation of the angular gyrus in visual perception. He alleges that it is connected with the sensibility of the globe of the eye and with the action of the ocular muscles. He states that in Monkeys in which he has excised this convolution the sensibility of the cornea of the opposite eye and also of the whole bulb is abolished, that the lateral movements of the eyes are incomplete, and that there is sometimes slight ptosis and lacrymation † Our experiments do not in the least confirm these statements. In every case in which we have destroyed one angular gyrus the sensibility of the conjunctiva of the opposite eye has been, so far as we could determine, in no way affected.‡ Not only is the reflex act of winking produced on touching the cornea, but the animal winces in a manner unmistakably indicative of pain. Where both angular gyri have been destroyed the result has been the same for both eyes.

Our experiments upon the temporo-sphenoidal or temporal lobe have been all, with one exception, performed bilaterally, for we very early came to the conclusion that no definite results were to be obtained in Monkeys regarding the senses of hearing, taste, or smell from unilateral lesions of the brain. Roughly speaking, we may class our experiments under two heads: (1) partial or local extirpations of portions of the lobe, (2) complete removal of the whole lobe. The partial extirpations comprised (*a*) the antero-inferior part of the lobe (cases 1 and 2), (*b*) the superior temporal gyrus (cases 1, 3, 7, and 11). They have produced in our hands no appreciable effect, neither loss of taste, smell, nor hearing, and, so far as could be determined in Monkeys, no diminution in the acuteness of any of these senses. Animals with the antero-inferior portion of the lobe, including the subiculum, completely cut away smell their food, immediately detect a malodorous substance, such as aloes or asafœtida, with which it (*e.g.*, a raisin) may have been smeared, and cast it aside without tasting. A raisin into which quinine has been inserted is smelt, eagerly bitten, and immediately rejected with expressions of disgust. Animals with both superior temporal gyri completely destroyed give evidence of the possession of acute powers of hearing; they turn at the slightest rustle, look up at the smallest noise, even immediately after the operation and when still drowsy from the prolonged influence of the anæsthetic, and follow with the head and eyes the direction of footsteps along a corridor outside the room in which they are confined. Some of these animals we have had under observation for many months; they have been seen and tested by many people, and the absence of the gyrus has been attested by *post-mortem* examination.

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* *Op. cit*, '4te Mittheilung,' pp 64, 65

† MUNK mentions that in Monkeys in which he has removed the angular gyri he has noticed, amongst other symptoms, that they employ the whole hand instead of the fingers merely to pick up small objects, and he infers from this that the movements of the eyeballs are interfered with. But it appears to us that such symptoms (which were not noticeable in our Monkeys) may more probably be explained by supposing that the adjacent ascending parietal gyrus, which contains the principal centres for the movements of the fingers, may have become partially involved in the lesion, especially since the operations were not performed antiseptically.

‡ In this point we are in agreement with LUCIANI and TAMBURINI, "Seconda Communicazione," 'Brain,' vol. 2.

Ferrier and Yeo* have published a similar case of destruction of the superior temporal gyrus on both sides of the brain with a result contrary to those which we have obtained. In their case the Monkey was apparently stone-deaf. It reacted to no sounds,† not even to the report of a pistol. The ears did not even twitch at unusual sounds, as they frequently do in Monkeys. It was examined independently by competent observers, and was exhibited at the International Medical Congress of 1881 to the Physiological Section, and no evidence of hearing even the report of a pistol could be obtained. The animal was kept under observation for thirteen months, and showed during all that time no clear evidence of hearing.

There is no doubt that Ferrier was justified by the result of this experiment in inferring that the cerebral localisation of auditory impressions is to be looked for in the superior temporal gyri.‡ But, to our thinking, he was not justified in assuming such localisation without further evidence than that afforded by this single experiment. The matter was of sufficient importance to call for a repetition of the lesion in other Monkeys; and had this been done by him we have no doubt, in view of our own experiments, that Ferrier would have seen reason to modify his too rapid conclusion. In six different Monkeys we have established this lesion, with or without involving other parts of the lobe, and in none of them has hearing been abolished, or even permanently diminished in acuteness.§ This discrepancy between the experiment of Ferrier and Yeo and these results of our own cannot be explained by assuming that the lesion was more extensive in their case than in ours. On the contrary, although in one or two of our animals a minute portion of the gyrus was found to have been left, in all without exception, as may be seen by comparing the respective figures, the removal was much more extensive and complete than in the Monkey operated on by Ferrier and Yeo, in which, especially upon the right side, a very noticeable amount of the convolution remains (see the figs. of sections across the brain in their paper already quoted. The photographs of the whole brain in the paper do not exhibit the limits of the lesion distinctly, but it is depicted in figs. 97 and 98, p. 309, of FERRIER'S 'Functions of the Brain.')

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* *Op. cit.*, Experiment 13; and Ferrier, 'Functions of the Brain.' pp. 309, 310

† This statement is, however, not unmodified. "Occasionally a doubt was raised as to whether the absence of reaction to sounds was absolute." Ferrier, *loc. cit.*, p 310

‡ This opinion must be modified since the publication of the notes of this case in a recent number of 'Brain.' (Ferrier: "Schafer on the Temporal Occipital Lobes." 'Brain,' April, 1888, pp. 13–16.) From these it appears that the Monkey frequently reacted to auditory impressions. The subject will, however, be fully discussed by me in the next number of 'Brain.'—[E.A.S., June 18, 1888.]

§ Dr. Ferrier was good enough to assist us on several occasions in investigating our animals, especially some of those with a double superior temporal lesion; and in all of those which we submitted to him, with one exception, he frankly acknowledged that the perception of auditory impressions

We are not, of course, called upon to explain the discrepancy, and can indeed offer no reasonable explanation, unless it be to assume that the Monkey which was selected by FERRIER and YEO for this operation happened, unknown to them, to be already deaf. At all events it would not appear that they put its hearing to the test before operating.* At the same time it must be admitted that there are great differences in perfectly normal Monkeys with regard to their reaction to sounds which they are unaccustomed to connect with any idea of danger. We have frequently observed that Monkeys which have experienced no cerebral lesion whatever will sometimes fail to start or show any sign of hearing at the report of a pistol, whilst others will react very strongly to such a noise. Thus the investigation is beset with difficulties, and it is only by the patient study of each individual and by the multiplication of instances that results to be relied on can be obtained.

One of our experiments (Monkey No. 6) involved the complete removal of the temporal lobe on both sides of the brain. How complete the lesion was is well shown both in the figures and in the casts of the brain † This is one of the cases in which there was, for a few days after the complete establishment of the lesion, a condition resembling idiocy produced, which, however, gradually passed away, leaving the animal in full and undoubted possession of all his senses. Taste, smell, and hearing were unquestionably present, and not only present, but, so far as could be determined, perfectly acute. The animal was repeatedly tested, and was, along with Nos. 5 and 11, submitted to special examination by a committee of the Neurological Society appointed for the purpose. Not the slightest doubt was possible as to the continued possession of these senses in this animal, and it is therefore not possible to suppose they are *localised* in the part of the brain which had been bilaterally removed. Whether there was any difference between this animal and normal Monkeys in the appreciation of the impressions obtained through those senses is a question regarding which we offer no opinion, nor is it possible, so far as we can see, to form such opinion from experiments upon animals. Considering only such manifestations as we are able to appreciate, the significance of these appears to favour no other conclusion than that at which we have arrived.

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remained—that the animals heard. The exception was No 5, as to the hearing of which we were not able to convince Dr. FERRIER, although we ourselves, from long and accurate observation of the animal, had no doubt whatever that it heard acutely. Curiously enough, it turned out on *post-mortem* examination that in this animal we had mistaken the convolutions, and removed on the left side of the brain the second temporal gyrus, leaving the superior intact.

* Since, as now appears (see preceding note), the Monkey was not really deaf *after* the operation, this [illegible] has become superfluous.

† [illegible] brains operated on are deposited in the Anatomical Museum of University College.

Lastly, we would offer a few remarks upon the two remarkable instances in which a bilateral lesion of the temporal lobe has produced a temporary general depression of the intellectual faculties, and has reduced the animals, for a time at least, to a mental condition resembling that of an idiot. In one of the cases (No. 6) this resulted on the complete removal of both lobes, but in the other (No. 12) on the removal of both superior gyri alone. It must, however, be remarked that in the latter instance the operation was conducted in such a manner as to produce a very profound lesion of that part of the hemisphere. The fissures bounding the gyrus (Sylvian and parallel) were drawn open, and the whole of the convolution, in its entire extent and depth, completely shelled out on both sides of the brain. A very great amount of vascular disturbance was thereby necessarily produced, and this must have affected, for a time at least, other portions of the brain.

Probably, therefore, the most reasonable explanation of the general depression of the intellectual faculties which these operations produced is to be found in this vascular disturbance. This, without actually causing the complete paralysis of function of the remainder of the cerebrum, which would have been evidenced by motor paralysis, may yet have sufficed to interfere with the active performance of its functions sufficiently to produce the results described. Thus, in both cases the movements were slow, the senses dulled, the memory very defective, and the disposition changed. It would obviously be unreasonable to assume, certainly in the second case, that these alterations are caused by the local lesion, but it appears to us that they may not unreasonably be explained on the hypothesis we have put forward. The gradual recovery of intelligence in both these animals is extremely interesting, and recalls instances which have been recorded in the human subject in which a gradual recovery has taken place after almost total abolition of the intellectual faculties *

The Arabic numbers attached to the figures illustrating this paper correspond to the Roman numerals in the record of cases. All the drawings have been made by tracing upon a plate of glass placed over the brain (arranged in an appropriate position) the outlines, the sulci, and the exact superficial extent of the lesion in each case. Such tracing has then been transferred to paper and filled in with appropriate shading. The representations of the sections have been prepared in like manner.

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* See for example a case which has been recorded by the late Professor W. SHARPEY in 'Brain,' vol. 2, under the title "The Re-education of the Adult Brain."

XII. *Further Observations on the Electromotive Properties of the Electrical Organ of* Torpedo marmorata.

By Francis Gotch, *Hon M A. Oxon., B A., B.Sc. London*

Communicated by Professor J. Burdon Sanderson, *F R.S.*

Received February 23,—Read March 8, 1888.

[Plates 51, 52.]

Introductory.

In my previous paper in the 'Philosophical Transactions,'[*] I have detailed the results of an investigation of the electromotive properties of the electrical organ of *Torpedo marmorata*, and I stated that I hoped to follow up the lines of inquiry indicated at various points in the account of that research.

My previous work had been done in the winter (January, 1887), and I was anxious to re-open the investigation at a time of year when Torpedoes could be readily procured, were in the most favourable state, and could be kept alive without any difficulty. This I was enabled to do in October, 1887, through the kindness of the Société Scientifique d'Arcachon, who placed at my disposal the rooms I had occupied in the previous winter, and to whom and the Society's Director, M. Durégne, I beg to offer my thanks for their aid.

Dr. Burdon Sanderson lent me the apparatus with which he and I had worked at Oxford and elsewhere, and with which I was well acquainted. The plan of work was to a great extent thought out before starting, and all the appropriate instruments taken to Arcachon from England. I had determined to attack especially one problem, in the hope that its solution would lead to a more extended view of the excitatory phenomena of the electrical organ. This problem was that opened up by du Bois-Reymond's remarkable discovery of what he terms the "irreciprocal conduction" manifested by the columns of the electrical organ.[†]

This subject has been already alluded to in my paper in the 'Philosophical Transactions,' and to that paper the reader must be referred for particulars as to the construction of the organ and the nature of du Bois-Reymond's experiments * The main features of the phenomenon in question may, however, be briefly described here, even at the risk of recapitulating what I have already published, in order to make the nature of the present investigation intelligible. In experimenting upon the effect of the passage of electrical currents, both voltaic and induced, through the organ, du Bois-Reymond observed that the organ itself exercised a remarkable influence upon the led-through currents. This was of such a character as to make it appear that the organ is a better conductor for a current directed through it in one particular direction than it is for any other led-through current; this favourable direction coincides with that of the current produced by the excitatory change of the organ itself: that is, of the "shock," or, as for the purpose of the present enquiry I prefer to term it, the "response." If, for instance, a strip of organ containing several columns be taken and connected by its ends, each still covered by an adherent patch of dorsal and ventral skin respectively, with a pair of non-polarisable electrodes, and through these and the strip an intense current of short duration be led first in one direction and then in the other, an inequality shows itself in the amount of the led-through current. This inequality is the more marked the shorter the duration and the greater the intensity (within certain limits) of the external led-through current, and is very marked, therefore, when this current is an induced current.

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[*] Gotch, "The Electromotive Properties of *Torpedo marmorata*," 'Phil. Trans.,' B, 1887, pp 487–537.

[†] Du Bois-Reymond, 'Archiv Anat. Physiol (Physiol. Abtheilung),' 1887, pp. 75; see also 'Biological Memoirs,' edited by J. Burdon Sanderson, pp. 500–532, Clarendon Press, 1887.

The conditions for performing the experiment with induced currents are extremely simple, and consist merely in connecting the tissue and electrodes to the galvanometer, the circuit passing through the secondary coil of an induction apparatus. The induction shock is now led through the strip and the galvanometer, first in one direction and then in the other. When it is directed through the tissue from the ventral to the dorsal surface, it has the same direction in the tissue as that of the shock or response, and the current is designated by du Bois-Reymond "homodromous." When directed through the tissue in the reverse direction, namely, from the dorsal to the ventral surface of the organ, it is termed "heterodromous.

Du Bois-Reymond finds that the galvanometric value of the homodromous current is always much greater than that of the heterodromous. The homodromous current must, therefore, either encounter less resistance in its passage through the tissue than the heterodromous does, or its electromotive force must be suddenly strengthened, and that of the heterodromous current weakened, presumably by the sudden establishment in the tissue of a new source of electromotive energy; du Bois-Reymond assumes that the first is the true explanation.†

In working with Dr. Sanderson in the summer of this year (1887) upon the properties and structure of the electrical organ in the tail of the Skate, the question of irreciprocity was entered upon. My previous work with the organ of the Torpedo

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* 'Phil. Trans.,' B, 1887, p. 491.

† E. du Bois-Reymond, 'Archiv Anat. Physiol. (Physiol. Abtheilg.),' 1887, pp. 98–104; see also 'Biological Memoirs,' edited by J. Burdon Sanderson, 1887, pp. 528–535.

had paved the way to the use of an experimental method which seemed to throw great light on the subject, and on finding this I determined to employ the same method in the present research. It is obvious that if the organ itself responds to the passage of an intense current of short duration, then within a few thousandths of a second after such a current is made there is an electromotive change set up in the organ which exactly fulfils the rôle of the hypothetical change the existence of which is required in the second alternative explanation. Being an excitatory phenomenon, it must always have the same sign, whether evoked by a homodromous or a heterodromous current, and must, in the case of the Torpedo organ, reinforce the former and diminish the force of the latter. My experiments on the nerve organ preparations had shown with what rapidity and intensity the electromotive change appeared, so that it was not improbable that DU BOIS-REYMOND's phenomenon might be entirely due to algebraic summation of several electromotive effects.

The experiments to be detailed conclusively prove that the organ of the Torpedo does respond to the passage through it of an induction shock, irrespective of its direction; and, further, that beyond the irreciprocal galvanometric effect due to allowing both the induction shock and the response of the organ to affect the instrument there is no such irreciprocity, the induction shock in both directions when the response is excluded being equal.

The experiments therefore show that the phenomena of "irreciprocal conduction" are in reality excitatory phenomena, the nature of which, from the method of investigation used, has not been recognised.

PART I.—DIRECT EXCITATION OF THE ELECTRICAL ORGAN BY INDUCED CURRENTS.

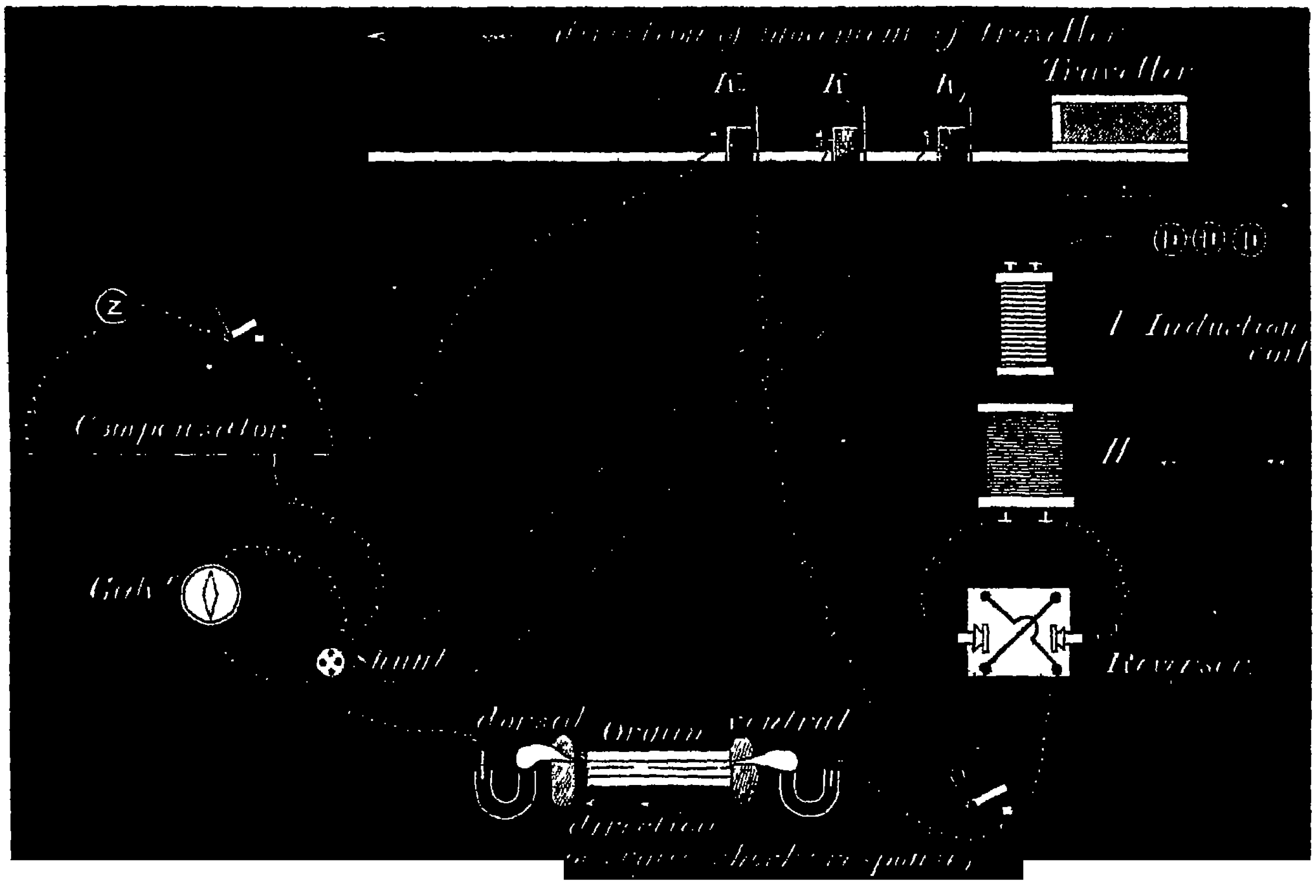
Method of Experiment.

The method employed in these experiments consisted in the use of a rheotome sufficiently accurate in its movement to enable the observer to connect the galvanometer with the tissue under investigation for a period of from two to three thousandths of a second, this period being capable of interpolation at any desired interval between the moment of the passage of the induction shock and five to six hundredths of a second after such passage.

The instrument used was the *Federmyographion* of DU BOIS-REYMOND, this being modified and furnished with three specially-constructed trigger keys.

The galvanometer previously used was now discarded, and a much more delicate instrument was employed. This instrument was a THOMSON reflecting galvanometer, made by ELLIOTT, having a resistance at 16° C. of 20,364 ohms. The light astatic system of the instrument has no aluminium vane to reduce the number of oscillations, but is made completely dead-beat by being enclosed between two thin plates of glass one-tenth of an inch apart. The circuit was arranged according to the plan given in fig 1, in which the keys K_1, K_2, and K_3 are shown. K_1 as the breaking key of the circuit of the primary coil of the induction apparatus, K_2 as a short circuiting key for the galvanometer, and K_3 as a key directly interposed between the tissue and the galvanometer, the opening of which thus opened the experimental circuit.

Fig 1.



This experimental circuit includes the secondary coil of the induction apparatus, a Pohl's reverser, and the usual compensating arrangement, four Callaud cells being employed as a steady compensating battery.

The induction apparatus was of the usual sliding kind, but with a scale graduated under the kind direction of Professor Kronecker; the numbers given to denote the position of the secondary coil thus bear strict comparison one with another.

Preliminary Experiments.

The first experiments were of a simple character, and were made with the view of ascertaining the existence of the inequality already referred to in the galvanometric readings of the homodromous, as compared with those of the heterodromous, led-through current. For this purpose a large Torpedo, measuring 46 centimetres in length and 32 centimetres in width, was taken, and, the electrical lobe having been destroyed, a mass of organ was removed with its skin surfaces still adherent. From this mass a strip was cut with a razor in the direction of the columns, care being taken to avoid the entry of the large electrical nerves; this strip was then sliced down and reduced to a narrow strip containing four or five uninjured columns, and measuring 40 millimetres in length by 5 millimetres wide and 5 millimetres broad.

It was placed upon a glass plate and led off by pads of kaolin moistened with 0·6 per cent. saline solution, applied to the ends of the strip to which a portion of the ventral and dorsal skin still remained adherent. This is shown on a small scale in fig. 1.

A similar method of preparation was used in all the following experiments. The pads were brought into connection with the U-tubes of the ordinary non-polarisable electrodes, and so with the experimental circuit.

The strip of organ showed a marked electromotive difference between its dorsal and its ventral ends, the "organ-current" previously described by me.* This organ-current was of the usual character, namely, such that the dorsal end of the columns was galvanometrically positive to the ventral, that is to say, the change was of the same sign as that which occurs when the tissue responds to excitation of its nerve. Such an electromotive change will be denoted all through this work by the sign +, which refers to the galvanometric condition of the dorsal electrode. This + effect subsided at first rapidly, then more and more slowly, and in half-an-hour was steady.

The first experiments having reference to the inequality in the led-through currents, the keys K_2 and K_3 were not used, the circuit being made independently of K_3 and kept closed.

The passage of the traveller of the rheotome opened K_1 at a fixed point in its movement, and thus ensured the development of a *similar* and *constant* induction shock. The break shock used was that caused by the opening of six GROVE cells placed in the primary circuit of the induction apparatus, the secondary coil standing at 1000. It was led through the electrodes, the tissue, and the galvanometer, first in the homodromous or (+) direction, and then in the heterodromous or (−) direction, and the galvanometric deflection noted.

The deflections were strikingly unequal, that of the (+) induction current being nearly three times as large as the (−).

Direction of induction current.	Galvanometer shunt.	Deflection.
Heterodromous (−)	$\frac{1}{100}$	− 55
Homodromous (+)	,,	+ 148
Heterodromous (−)	,,	− 54
Homodromous (+)	,,	+ 146

Here then was the "irreciprocal conduction" which DU BOIS-REYMOND had observed, and which I had failed to obtain evidence of in my previous experiments.

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* GOTCH, 'Phil. Trans.,' B., 1887, pp. 502, 503.

A preliminary experiment was now made in which the induction shock was made to traverse the tissue, but was not allowed to affect the galvanometer. To effect this the key K_2 was used and was placed at 1/100″ distance from K_1, the galvanometer was thus short-circuited for the first hundredth of a second after the passage of the induction shock. Under these conditions both induction shocks, (+) and (−), were followed by an electromotive effect of the same sign, namely, that of the excitatory response of the organ, and therefore +

Induction shock direction	Time of closure of galvanometer	Shunt.	Deflection.
(+)	·01″ after shock	$\frac{1}{100}$	+ 41
(−)	,,	,,	+ 19
(+)	,,	$\frac{1}{10}$	+ 475
(−)	,,	,,	+ 228

The signs $\frac{1}{100}$, $\frac{1}{10}$, indicate that by means of an appropriate shunt only one-hundredth or one-tenth of the total effect passed through the galvanometer.

It was now necessary to use the rheotome and determine the time relations of this effect. For this purpose a vigorous female Torpedo was killed the next day, measuring 38 × 25 centims. A strip was prepared, as before, from the median edge of the organ; it measured 60 × 10 × 10 millims. The organ current, considerable at first, was allowed to subside until it became steady. Temperature of organ 15° C. The rheotome was used with all three keys, and the following Table shows the result :—

Galvanometer shunt	Direction of induction current through tissue.	Time of closure of galvanometer circuit.				
		K_2-K_3 0″–005″	K_2-K_3 005″-·015″	K_2-K_3 015″-025″	K_2-K_3 ·025″-035″	K_2-K_3 035″-·045″
$\frac{1}{100}$	(+)	+ 142	+ 45	+ 40	+ 20	+ trace
,,	(−)	− 141	+ 245	+ 100	+ 38	+ 4

It is evident that there is no difference in the galvanometric value of the two induction shocks when the galvanometer circuit is so arranged as to exclude any succeeding change in the tissue. With a closure of from 0″ to ·005″, there is no inequality. During the next period of closure from ·005″ to ·015″, however, an electromotive change of considerable intensity occurred in the tissue, which, in this particular instance, was more pronounced after the (−) than after the (+) induction current; the effect was +, and had its maximum somewhere about 1/100″ after the induction shock, whilst it lasted as long as 4/100″. An experiment was now made in order to ascertain more minutely the time relations of this excitatory effect. For this purpose the keys of the rheotome were arranged so as to secure a closing time of the galvanometer circuit of only 25/10,000″, the first 1/100″ was thus subdivided into four periods

Two Groves in primary; secondary coil, 3000.

Galvanometer shunt.	Direction of induction current	Time of closure of galvanometer			
		K_2–K_3 0″-·0025″	K_2–K_3 ·0025″-005″	K_2–K_3 005″-0075″	K_2–K_3 0075″-01″
$\frac{1}{100}$	(+)	+ 230	+ 15	+ 20	+ 123
,,	(−)	− 230	− trace	+ 55	+ 251

In this case the induction shocks in both directions were equal, as is shown by the readings when the closure of the galvanometer circuit was arranged to include the induction shock only, that is, when the closure was from 0″ to ·0025.″ In the next, the second, period, changes occur indicating the algebraic summation of the commencing tissue change with the remainder of the induction shock. The third period shows the commencement of a marked + change in the tissue, which in the fourth period has attained a very great intensity, being as pronounced a galvanometric effect in one case, even with this short closure, as the induction shock itself. There can be only one source of such a change, and that is the excitatory process of the organ itself; the change resembles that which occurs in the organ when the nerve trunk supplying it is excited, and the strip of tissue apparently responds in a similar manner, whether the trunk or the endings of the nerve are excited.

It is clear now what must happen if the induction shock and the subsequent response are both allowed to affect the galvanometer. Thus in this case the following experiment shows how the two currents will combine to give one galvanometric effect:—

Galvanometer shunt.	Direction of induction current	Time of closure of galvanometer circuit.		
		K_2–K_3 0″-·005″	K_2–K_3 005″-015″	K_2–K_3 0″-·01″
$\frac{1}{100}$	(+)	+ 231	+ 240	+ 405
,,	(−)	− 231	+ 460	+ 80

The examination of the first hundredth of a second having been thus made, the experiment was continued along broader lines, and a succession of readings obtained which indicated the general characters and duration of the excitatory effect A long period of closure, 1/100″, was used, and the results are given in the subjoined Table.

Two GROVES in primary; secondary, 3000.

Shunt.	Direction of induction current	Time of closure of galvanometer circuit					After-effect.
		K_2-K_3 005″- 015″	K_2-K_3 015″-·025″	K_2-K_3 025″- 035″	K_2-K_3 035″- 045″	K_2 K_3 045″- 055″	K_2 only. 055″ onwards
$\frac{1}{100}$	(+)	+ 297	+ 161	+ 26	+ 10	+ 8	+ 20
,,	(−)	+ 448	+ 162	+ 35	+ 6	+ 5	+ 41

The large electromotive effect is thus seen to subside from its maximum, first rapidly and then slowly, and it is followed by an electromotive change in the tissue of similar sign, the after-effect. A corroborative experiment, selected out of many, all of the same character, may be briefly given. It was made on a strip of organ, prepared as has been previously indicated and led-off as before; the strip was 58 millims. × 6 × 6. The results of the rheotome readings may be divided into three groups, as follows.—

I. MINUTE Analysis of Events of first $\frac{1}{100}$″. Two GROVES in primary; secondary coil, 3000. Temp. 15° C.

Galvanometer shunt	Direction of induction current.	Time of closure of galvanometer circuit				
		K_2-K_3 ·0″-·0025″	K_2-K_3 ·0025″- 005″	K_2-K_3 005″- 0075″	K_2-K_3 0075″- 01″	K_2-K_3 01″- 0125″
$\frac{1}{100}$	(+)	+ 220	+ 4	+ 90	+ 145	+ 40
,,	(−)	− 220	− 6	+ 35	+ 206	+ 51

II. GENERAL Analysis of Events of $\frac{5}{100}$″.

Galvanometer shunt.	Direction of induction current.	Time of closure of galvanometer circuit					After-effect.
		K_2-K_3 005″-·015″	K_2-K_3 015″-·025″	K_2-K_3 ·025″-·035″	K_2-K_3 ·035″- 045″	K_2-K_3 045″-·055″	K_2 only 055″ on
$\frac{1}{100}$	(+)	+ 302	+ 65	+ 20	+ 5 (G $\frac{1}{10}$ 46)	G $\frac{1}{10}$ + 45	G $\frac{1}{10}$ + 430
,,	(−)	+ 345	+ 95	+ 25	+ 10 (G. $\frac{1}{10}$ 95)	G. $\frac{1}{10}$ + 70	G. $\frac{1}{10}$ + 455

III. The After-effect from 1″ onwards.

Galvanometer shunt.	Direction of induction current	Time of reading of galvanometer			
		1″-5″	at 20″	at 35″	at 50″
$\frac{1}{10}$	(+)	+ 320	+ 130	+ 95	+ 40
„	(−)	+ 210	+ 105	+ 60	+ 31

The prolonged after-effect in Table III was obtained by closing the circuit 1″ after the passage of the rheotome; the needle swung out and attained its limit of deflection by 5″; its position was then noted as it returned towards zero every 15″, the falling time of the needle itself being 10″.

A comparison of the features of this electromotive change with that obtained in the case of the nerve organ preparation, as given in my previous paper, leaves no doubt that we have here to deal with an excitatory response of similar nature.

In my former experiments I had observed how greatly changes of temperature influence the time relations of the nerve organ response. It was therefore advisable to ascertain if this direct response of the tissue was similarly affected.

Effect of Temperature upon the Response to Direct Excitation.

The method of warming or cooling strips of organ consisted in the use of a metal stage covered with tissue paper soaked in melted paraffin, through which water at different temperatures was allowed to run; but it was subsequently found necessary to adopt a more rapid and effectual plan. This consisted in placing the organ columns upon a previously warmed tile, the temperature of which was kept up by its end being immersed in the water of a small water bath. For cooling, the tile was removed and the strip allowed to rest upon a slab of ice suitably hollowed out to receive it, the surface of which was covered with tissue paper previously soaked in paraffin. The temperature of the organ itself was readily ascertained by placing upon an organ mass the bulb of a thermometer.

Five separate experiments are selected to illustrate the striking effects of temperature, and it will be noticed in all these experiments that there is no inequality between those (+) and (−) galvanometric deflections obtained at the same temperature during the period of closure 0″ to ·0025″; that is to say, that there is no evidence of "irreciprocity" when the induction shock, and that only, is allowed to affect the galvanometer.

EXPERIMENT 1. Large Torpedo, 45 × 32 centims. Strip 50 × 10 × 8 millims Galvanometer shunt $\frac{1}{100}$. Two GROVES in primary; secondary at 4000.

Temperature of organ.	Direction of induction current	Time of closure of galvanometer circuit					
		K_2-K_3 0″– 0025″	K_2-K_3 0025″– 005″	K_2-K_3 ·005″– 0075″	K_2-K_3 0075″– 01″	K_2-K_3 01″– 0125″	K_2-K_3 0125″– 015″
15° C	(+)	+ 279	+ 12	+ 45	+ 185	+ 98	
	(–)	– 280	+ 17	+ 22	+ 181	+ 124	
20° C	(+)	+ 306	+ 98	+ 132	+ 60		
	(–)	– 304	+ 48	+ 136	+ 75		
10° C.	(+)	+ 275	+ 6	+ 23	+ 131	+ 85	+ 18
	(–)	– 275	– 8	+ 18	+ 147	+ 98	+ 17

It is evident that the time relations of the response are considerably affected by temperature; thus we find that with a temperature of 20° C. the response is present from ·0025″ to ·005″ after the passage of the induction shock. Accordingly, we should expect that a closure of from ·0″ to ·005″, including, as it must, both induction current and response, would show the so-called irreciprocity in the warmed, but not in the cooled, tissue. Such is the case, as the following Table shows .—

GALVANOMETER $\frac{1}{100}$ shunt.

Temperature of organ.	Direction of induction current.	Period of closure.	
		K_2-K_3 0″–·005″	K_2-K_3 ·0″–·01″
22° C.	(+)	+ 338	+ 475
	(–)	– 290	– 12
8° C	(+)	+ 270	+ 380
	(–)	– 270	– 174
22° C	(+)	+ 390	
	(–)	– 267	

It is so obvious that algebraic summation must thus cause "irreciprocity" that further instances of this kind need not be given in the succeeding experiments.

EXPERIMENT 2. Large Torpedo, 45 × 32 centims. Strip 51 × 5 × 5 millims. Galvanometer $\frac{1}{100}$ shunt. Two GROVES in primary; secondary coil at 4000.

Temperature of organ	Direction of induction current	Time of closure of galvanometer circuit.						
		K_2-K_3 ·0″– 0025″	K_2-K_3 0025″–·005″	K_2-K_3 005″–·0075″	K_2-K_3 0075″–·01″	K_2-K_3 01″–·0125″	K_2-K_3 0125″– 015″	K_2-K_3 ·015″– 0175″
15° C	(+)	+ 290	+ 23	+ 70	+ 235	+ 120	+ 30	
	(−)	− 290	− 18	+ 55	+ 165	+ 75	+ 16	
22° C.	(+)	+ 330	+ 101	+ 110	+ 26			
	(−)	− 322	+ 48	+ 106	+ 18			
6° C.	(+)	+ 298	+ 10	0	+ 88	+ 125	+ 56	+ 5
	(−)	− 298	− 12	0	+ 91	+ 115	+ 52	+ 6

EXPERIMENT 3. Large Torpedo, 48 × 31 centims. Strip 55 × 8 × 10 millims. Galvanometer $\frac{1}{100}$ shunt. Two GROVES in primary; secondary coil at 10000.

Temperature of organ.	Direction of induction current.	Time of closure of galvanometer circuit.									
		K_2-K_3 0″ to 0025″	K_2-K_3 0025″ to ·005″	K_2-K_3 ·005″ to 0075″	K_2-K_3 ·0075″ to ·01″	K_2-K_3 ·01″ to ·0125″	K_2-K_3 0125″ to 015″	K_2-K_3 ·015″ to ·0175″	K_2-K_3 ·0175′ to ·02″	K_2-K_3 ·02″ to ·0225″	K_2-K_3 ·0225″ to 025″
15° C	(+)	+ 271	+ 8	+ 65	+ 395	+ 235	+ 76	+ 25	+ 40	+ 25	
	(−)	− 272	− 8	+ 51	+ 428	+ 290	+ 68	+ 60	+ 110	+ 45	
22° C	(+)	+ 395	+ 90	+ 91	+ 78	+ 64					
	(−)	− 393	+ 85	+ 95	+ 40	+ 20					
3° C.	(+)	+ 217	+ 3	0	0	0	+ 8	+ 54	+ 102	+ 161	+ 136
	(−)	− 216	− 4	0	0	0	+ 22	+ 65	+ 178	+ 203	+ 189

EXPERIMENT 4. Large Torpedo, 62 × 38 centims. Strip 65 × 15 × 10 millims. Galvanometer $\frac{1}{100}$ shunt. Two Groves in primary; secondary coil at 5000.

Temperature of organ.	Direction of current.	Time of closure of galvanometer.			
		K_2-K_3 ·0″–·0025″	K_2-K_3 ·0025″–·005″	K_2-K_3 ·005″–·01″	K_2-K_3 ·01″–·0125″
15° C.	(+)	+ 495	+ 31	+ 18	+ 276
	(−)	− 495	− 32	+ 10	+ 187
23° C.	(+)	+ 585	+ 130	+ 125	
	(−)	− 584	+ 10	+ 82	

EXPERIMENT 5.—Large Torpedo, 52 × 37 centims. Strip 60 × 12 × 8 millims. Galvanometer $\frac{1}{100}$ Three GROVES in primary; secondary coil at 5000.

Temperature of organ.	Direction of induction current	Time of closure of galvanometer circuit.								
		K_2–K_3 0″ to 0025″	K_2–K_3 0025″ to 005″	K_2–K_3 005″ to 0075″	K_2–K_3 0075″ to 01″	K_2–K_3 01″ to 0125″	K_2–K_3 0125″ to 015″	K_2–K_3 015″ to 0175″	K_2–K_3 0175″ to 02″	K_2–K_3 02″ to ·0225″
15° C.	(+)	+ 483	+ 9	+ 178	+ 434	+ 271	+ 69	+ 29	+ 22	
	(−)	− 484	− 7	+ 70	+ 206	+ 171	+ 95	+ 15	+ 11	
2° C	(+)	+ 382	+ 6	0	0	0	0	+ 7	+ 15	+ 22
	(−)	− 381	− 6	0	0	0	0	+ 5	+ 10	+ 12
10° C	(+)			0	+ 149	+ 231	+ 81	+ 35	+ 14	

These experiments show that rise of temperature accelerates and fall of temperature delays the commencement of the excitatory change following direct electrical excitation of the organ.* A glance at the curves given in Plate 51 at the end of this treatise shows how completely cold separates the induction shock from the subsequent response, and how warming brings the two galvanometric effects together; the interval of time which elapses between the two is the "period of delay" or "latent period" and is at its shortest, *i.e.*, at 20° C., more than ·0025″. However favourable the conditions, with transmission time excluded by the method of experiment, it would therefore appear that there is an interval of time between excitation and response. This interval may be regarded as the sum of the time necessary for the establishment of the excitatory process in the nerves *plus* that necessary for the development of those chemical changes in the protoplasm of the organ which may lie at the bottom of the obvious electromotive effect. It has been previously pointed out that in the case of the nerve organ preparation the fact that changes in the temperature of the organ affect the length of this period would seem to require the existence of this second factor, for, under the most favourable circumstances and after deducting the time occupied in nerve transmission, there remained an interval of 4/1000″ between excitation of the nerve trunk and the response of the organ. In the present experiments the earliest effect was observed with a closure of from ·0025″ to ·005″; and, as the conditions of these experiments excluded loss of time due to nerve transmission, the existence of a period of delay must be regarded as certain.

Although the passage of an induced current through the columns of the electrical organ evokes an excitatory response of the tissue, it is, however, doubtful if the expression "direct" excitation is a strictly correct one as applied to this phenomenon. In the case of muscle there exists a method (curarisation) by which the nervous channels may probably be eliminated; this is, however, not applicable to the electrical organ. It was shown by MOREAU * that in a curarised and immobile fish the organ was still capable of responding by a vigorous reflex discharge to external stimulation of the skin. I have made numerous experiments which have confirmed this fact; indeed, the smartest shock I ever received was from a medium-sized curarised Torpedo, which I grasped when quite immobile between my hands. On dissecting out the nerves I found that electrical stimulation of the spinal cord and motor nerves produced no muscular contractions, whilst vigorous electrical responses of the organ followed excitation of the electrical nerves. The fish were readily curarised in from two to three hours by the injection of 0·5 cub. centim. of a 1 per cent. solution under the dorsal skin near the tail. This being the case, it was certain that the strip of curarised organ would respond, like the uncurarised, to the passage of an induction shock, as was found to be the case. It is, therefore, not improbable that the stimulation of the column by an induction current is not analogous to the direct electrical excitation of curarised muscle, but to that of nerve, it being an excitation of the innumerable nerve branches which pervade the transverse protoplasmic septa of the column rather than the protoplasm of the septa. The singular curare failure would seem to me to point to the conclusion that an electrical organ is pre-eminently a structure in which an immense number of nerve endings are grouped together into a system, and that the excitatory electromotive change may be nothing more than the fact that when an excitatory process travels down a nerve its trunk becomes negative to its terminal cross-section. Although such an effect is relatively feeble in each ultimate fibril, the enormous quantity of fibrils may augment its intensity, even to the height attained by the electromotive change of an electrical column. If an electromotive change in the protoplasmic plates, as distinct from that in the nerves, is to be looked for, then I venture to think that it may be found in that remarkable prolonged "after-effect," details of which have been given in my previous communication.†

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* The experiments also show that the resistance of the preparation and the electrodes diminishes as the temperature rises, as is evidenced by the value of the readings given in the first column.

Effect of Strength and Direction of Exciting Current.

The discovery of the response of the strip of organ is entirely due to the use of the rheotome method, for without it the induction shock masks the response. It is, therefore, essential to use the rheotome even in such simple experiments as those necessary for ascertaining how far the column responds to induction shocks of different strength. As, however, we are now only concerned with the amount of the response evoked, it is sufficient to take one definite time of closure, which, while excluding the induction current, shall include at ordinary temperatures the maximum of the response. The period of closure selected was from ·005″ to ·015″; the induction shock used was the break of 3 GROVES, its intensity being varied by the position of the secondary coil. With the secondary coil at 3000, the shock gave when led through

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* MOREAU, 'Annales des Sciences Naturelles (Zoologie),' vol. 18, 1862, pp. 12–14.

† *Loc. cit.*

10,000 ohms and the galvanometer (1/100 shunt) a deflection of 332 scale. If 1/3000 of this strength is taken as unity, then the numbers in the Table give relative strengths.

Galvanometer shunt	Intensity of induction current	Direction of induction current	Closing time K_2-K_3.	Deflection.
$\frac{1}{10}$	Secy 100	(+)	005″-015″	0
„	100	(−)	„ „	0
„	200	(+)	„ „	+ 23
„	200	(−)	„ „	+ 20
„	300	(+)	„ „	+ 65
„	300	(−)	„ „	+ 40
„	400	(+)	„ „	+ 174
„	400	(−)	„ „	+ 155
„	500	(+)	„ „	+ 390
„	500	(−)	„ „	+ 395
$\frac{1}{100}$	600	(+)	„ „	+ 45
„	600	(−)	„ „	+ 48
„	1000	(+)	„ „	+ 102
„	1000	(−)	„ „	+ 100
„	1500	(+)	„ „	+ 235
„	2000	(+)	„ „	+ 300
„	2500	(+)	„ „	+ 402
„	3000	(+)	„ „	+ 508
„	3500	(+)	„ „	+ 530

The Table shows that the magnitude of the response increases with increasing strength of induction shock, resembling in this particular the behaviour of the organ to excitation of its nerve.

The relation of the response to the *direction* of the exciting current is by no means so simple, since different results have been obtained under apparently similar conditions. This much, however, is certain, that the most effectual exciting current is one which traverses the entire length of a column, and that it is generally most effectual when (+), *i.e.*, directed through the column from the ventral to the dorsal aspect. An analysis of all the instances noted will make this clear; the instances fall into three groups.

Galvanometer shunt $\frac{1}{100}$	I. Most favourable direction of induction current (+). 14 cases	II Both induction currents (+) and (−) equally effectual. 4 cases.	III Most favourable direction of induction current (−) 4 cases
Closing time	(+) (−)	(+) (−)	(+) (−)
005–015	+ 255, + 145	+ 429, + 411	+ 220, + 375
" "	+ 455, + 311	+ 398; + 375	+ 45; + 245
" "	+ 465, + 320	+ 390, + 395	+ 771; + 837
" "	G $\frac{1}{1000}$ + 92, + 74	+ 156, + 142	+ 160; + 305
" "	+ 780, + 565		
" "	G $\frac{1}{1000}$ + 82, + 68		
" "	+ 229, + 143		
" "	+ 324, + 196		
" "	+ 448, + 305		
" "	+ 434; + 206		
" "	+ 90, + 60		
" "	+ 585, + 412		
" "	+ 342; + 215		
" "	+ 300, + 124		

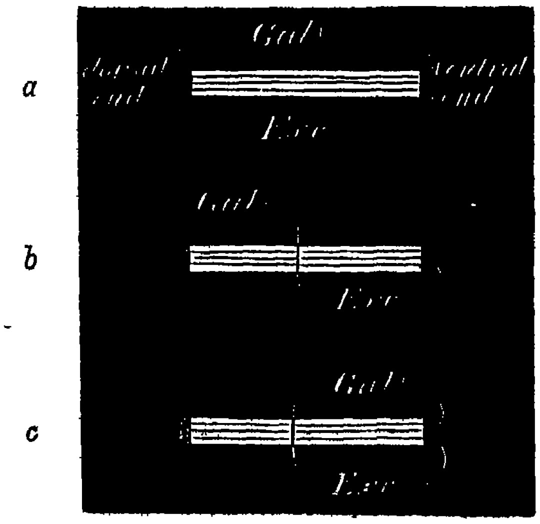
The question of the influence of the direction of the current on the effect is probably in relation with ECKHARD's discovery that the nerve organ preparation responds more fully when the trunk of the nerve is excited by an induction shock, if the induction shock be descending. The (+) induction current through the organ is a descending one as far as the finer nerve fibrils are concerned. It must, however, often happen that a preparation includes a large trunk of nerve which may first run from the dorsal towards the ventral end before dividing into its branches. Although no satisfactory evidence of this being the cause of the greater efficiency of the (−) led-through current observed in certain exceptional instances was obtained, it seems probable that this is the explanation of the anomalous cases.

If the induction current be directed across a strip which is led off by its two skin-covered ends, then a very feeble excitatory + change is seen; thus, to give an instance, it was in one case (G 1/10 shunt) + 33 with a rheotome closure of from ·005″ to ·025″; whereas the excitation of the whole strip in the usual way gave (G. 1/100) + 585. Occasionally, however, it happened that the cross excitation evoked a much larger response; on examination, it was found that the strip of organ included between its columns the large trunk of a nerve, and that mechanical injury of the tissue containing this nerve produced the same response. It was thus clear that this was a case of nerve trunk excitation. This leads naturally to the consideration as to how far the response can be localised to the part of the column traversed by the induction shock. The experiments to be now referred to show that the response is absolutely localised to the led through tract. From what has been said, it is of great importance to prepare strips of organ in such a way as to avoid the inclusion in the strip of an obvious nerve trunk. In order to secure this the nerves with their main branches were carefully dissected out, and the part of the organ not cut into by the dissection was used for experimental purposes.

Limitation of Response to Tract of Tissue through which the Current passes

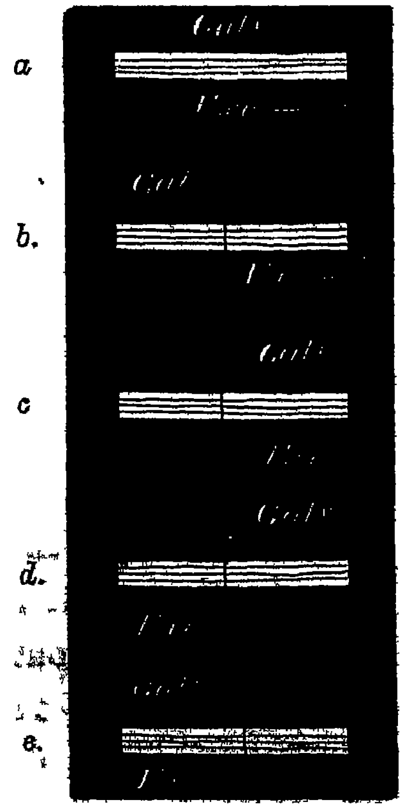
The plan of experiment consisted in the use of two circuits and two pairs of non-polarisable electrodes, one pair *Exc.* being connected with the secondary coil, the other pair *Gal.* being connected with the galvanometer The galvanometer contacts could thus be placed either within or just outside the led-through tract, this latter being confined in this instance to either the ventral or the dorsal half of the organ columns. The usual kaolin pads were used for leading off, and in addition a loop of thick thread steeped in saline solution was loosely tied round the equator of the strip of organ; the kaolin pads were in contact with the skin covered ends. The results of two such experiments are shown in the following Table —

TORPEDO 52 × 37 centims. Strip 56 × 8 × 10 millims. Period of Galvanometer closure always ·005″ to ·025″.



Induction shock		Shunt	Deflection
a	(+)	$\frac{1}{100}$	+ 90
	(−)	”	+ 60
b	(+)	$\frac{1}{10}$	0
	(−)	”	0
c	(+)	$\frac{1}{100}$	+ 26
	(−)	”	+ 16

ANOTHER strip of organ 58 × 7 × 10 millims.



Induction shock		Shunt	Deflection
a	(+)	$\frac{1}{100}$	+ 260
	(−)	”	+ 405
b	(+)	$\frac{1}{10}$	− trace
	(−)	”	”
c	(+)	$\frac{1}{100}$	+ 105
	(−)	”	+ 68
d	(+)	$\frac{1}{10}$	− 15
	(−)	”	− 26
e.	(+)	$\frac{1}{100}$	+ 168
	(−)	”	+ 330

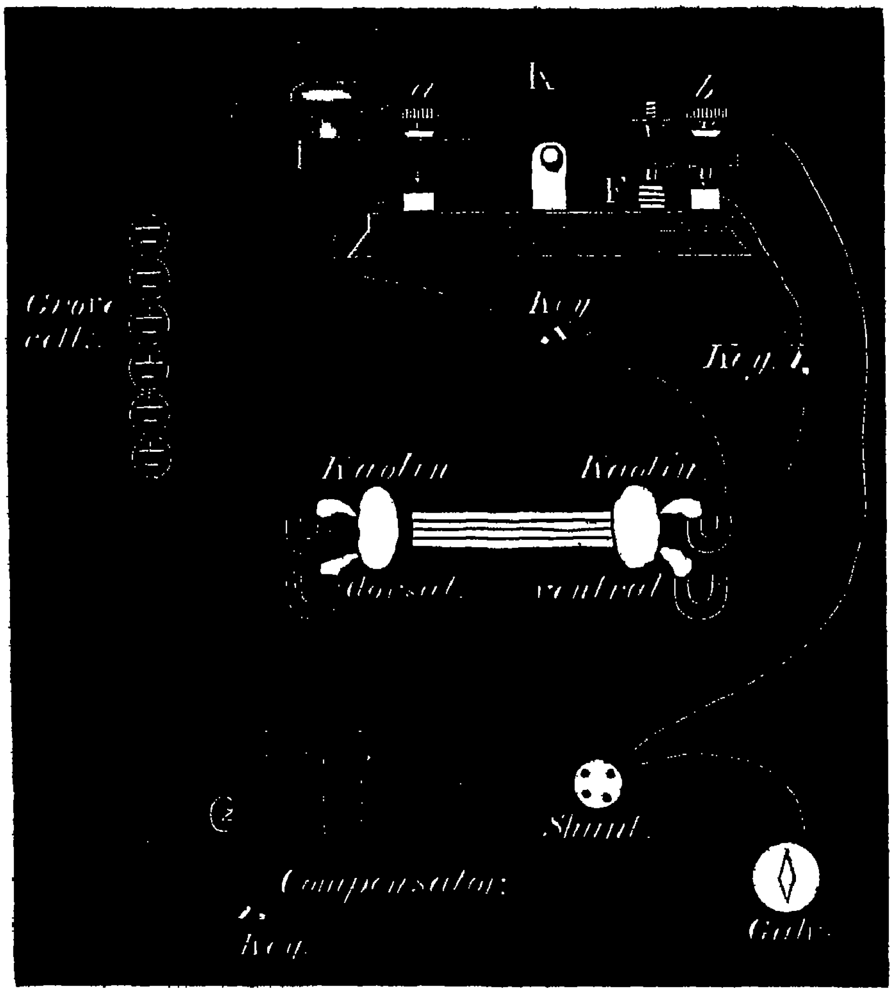
The — effect observed in extrapolar leading-off is undoubtedly due to the spread of the current of the response. The experiment is conclusive as showing that a large response may be evoked which is confined to the led-through tract. *There is thus no propagation of the excitatory state from one plate to another.* This most important fact has its cause in the structure of the organ.

Whatever may be the microscopic characters of the nerve terminations in the plates, and the part which they play in the production of the excitatory electromotive change, there is no evidence of any continuity of protoplasm between one plate and its neighbours. It appears that each plate is physiologically completely severed from all other plates. In order, therefore, to secure the simultaneous response of a whole column, either the nerve trunk supplying the column must be excited or an induction shock must traverse all the septa of the column.

Experiments referring to Excitation by the Voltaic Current

The use of the rheotome has thus revealed the fact that the passage of an induction current through a strip of organ excites the tissue. In no single instance was such an excitatory phenomenon found to be absent. This being the case, it is evident that unless care is taken to exclude this excitatory effect from influencing the galvanometer, the passage of an induction current in opposite directions must be attended by unequal galvanometric deflections. It is therefore essential to know, with regard to DU BOIS-REYMOND's experiments with induction currents, whether he used a rheotome which would exclude the response. There is no indication in his published works of his having done so; whilst in the case of the voltaic current the duration of his shortest closing time is given as ·03″. This must therefore include both the voltaic current and any response, and the inequality noted may be thus accounted for. It is moreover clear, as regards induction shocks, that, apart from the summation of exciting current and excitatory response, there is no evidence of there being any inequality as dependent upon their direction. I have made twenty-six distinct observations on very vigorous fish, and, with the response excluded by closing the galvanometer circuit from 0″ to ·0025″ only, no irreciprocity in DU BOIS-REYMOND's sense was observed; but, as a large number of DU BOIS-REYMOND's experiments were made with voltaic currents of considerable intensity and short duration, it was desirable to ascertain whether the passage of such currents through the organ did evoke a response. The difficulties of obtaining a satisfactory reply to this inquiry were instrumental, and the experiments are therefore by no means conclusive. I had no instrument of sufficient accuracy to enable me to pass a very short intense voltaic current of known duration through the tissue, since, for this purpose, it was essential that the galvanometer circuit should be completely broken during the passage of the voltaic current. The rheotome was not therefore practicable, and I had to use a very well-made double key with extremely well-insulated junctions. The key was a see-saw key which broke one circuit whilst it closed another. The arrangement adopted will be rendered clear by the diagram in fig. 2; the key (K) is introduced into the circuit so that a tap will cause a short closure of the voltaic current at *a*, whilst the galvanometer circuit is broken at *b*; the strong spring, F, ensures the closure of the galvanometer circuit about 2/100″ after the short closure of the voltaic current. By means of another key worked by hand, the galvanometer circuit was again broken 1″ after the striking of K. The experiments were repeated at intervals of two minutes. The passage of the voltaic current was followed by considerable polarisation, which, in the case of the (−) current would obscure the effect of an excitatory response, since both

Fig 2



would have the same sign, +. It was, however, easy to distinguish between the + excitatory response and the − polarisation effect which succeeded the passage of the + voltaic current, especially as the galvanometer circuit only remained closed for 1″. Torpedo 46 × 32 centims.; Strip 51 × 10 × 10 millims.

7 Groves,	direction	(+)	Galv.	$\frac{1}{100}$	+ 520
"	"	(+)	"	"	+ 410
"	"	(+)	"	"	+ 60
"	"	(+)	"	$\frac{1}{10}$	+ 460
"	"	(+)	"	"	+ 150
"	"	(+)	"	"	+ 170

The (+) current thus produces a + after-effect; and, since a longer duration of (+) current is sufficient to give nothing but − effects, whilst the short tap gives a + effect, it would appear that in this case an excitation had occurred at closure The reversal of effect is very striking, and shows that with the long closure the + effect had passed off before the galvanometer circuit was connected up again

Tap	closure.	7 Groves,	direction	(+)	Galv	$\frac{1}{10}$	+ 50
1″	„	„	„	(+)	„	„	− 52
Tap	„	„	„	(+)	„	„	+ 30
1″	„	„	„	(+)	„	„	− 40
Tap	„	„	„	(+)	„	„	+ 43
1″	„	„	„	(+)	„	„	− 25
Tap	„	„	„	(+)	„	„	+ 32

In another preparation, the opening of the current appeared to be followed by excitation and polarisation effects, as the subjoined details show :—

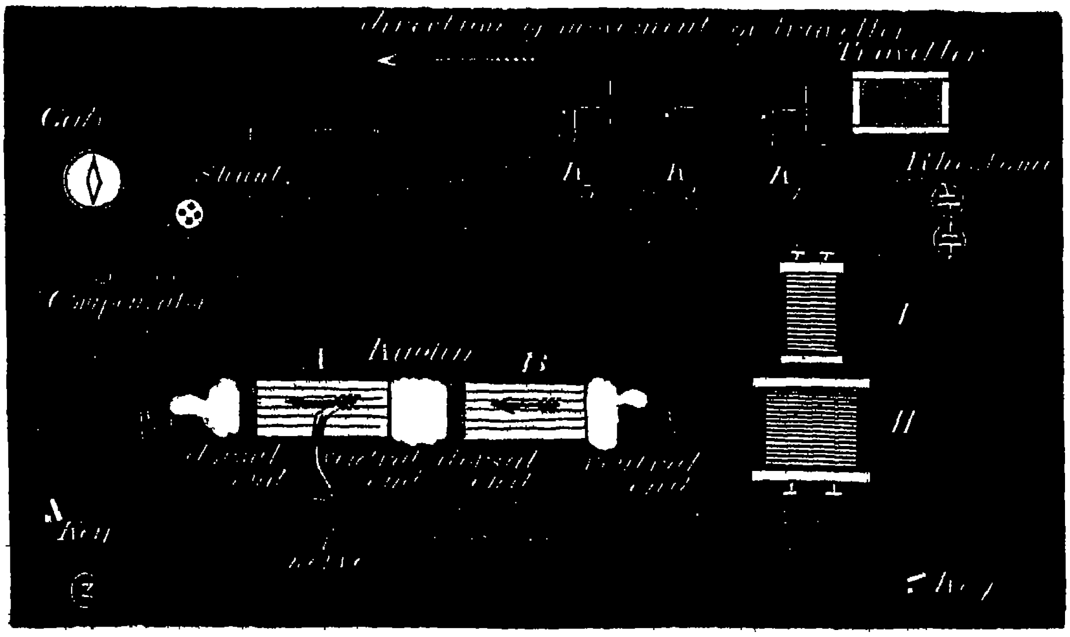
Tap	closure	7 Groves,	direction	(+)	Galv.	$\frac{1}{100}$	+ 150
$\frac{1}{4}$″	„	„	„	(+)	„	„	+ 80 − 10
$\frac{1}{2}$″	„	„	„	(+)	„	„	+ 50 − 25
1″	„	„	„	(+)	„	„	+ 30 − 45
2″	„	„	„	(+)	„	„	+ 20 − 60
			„	(+)	„	„	+ 15. − 120

It is probable that the voltaic current does excite the strip, just as the induction current does; and, if an excitatory change is evoked by the passage through the tissue of an intense current, then the meaning of du Bois-Reymond's results with the voltaic current would seem to be that he obtained a summation of voltaic current and the current of the excitatory change.

Part II.—Excitation of the Electrical Organ by the Current of its own Response.

Since the organ responds to the passage through its columns of an intense current led through them in the direction of their length, and since such response consists essentially of an electromotive change such that a current traverses each column in the direction of its length, of an intensity almost comparable with that of an induction shock, it follows that the tissue ought to be excited to a further secondary response by the current of its own primary response. If this should be the case, then every response must be of a reverberating character, the initial excitatory change itself producing a secondary feebler one, this a tertiary, still feebler, and so on, the tissue echoing the primary explosion until the individual replies become too faint to be followed. The experiments to be detailed show that this is indeed the true character of the nerve organ response in vigorous summer fish. Before proceeding to set forth these, the following experiments with two separate strips of organ must be referred to. These show that it is possible to evoke a response in a strip of organ by the passage through it of the excitatory electrical current produced by the response of a nerve organ preparation A nerve organ preparation, A, was made, and the ends of its columns led off by saline kaolin pads. It was excited by electrical stimulation of its nerve at some distance from the tissue, the exciting current being the break induction shock caused by the break of K_1. The current of its response did not proceed directly to the galvanometer circuit, but was led lengthwise through the columns of an interposed separate isolated strip of organ, B, the general arrangement of the circuit being shown in fig. 3. This strip, B, could be placed either so that, if it responded, its

Fig 3



response should augment that of A, or so that its response should diminish that of A, as will be seen by a glance at the diagrams accompanying the experimental details. The very first experiment made upon the tissue of a vigorous fish showed that the secondary strip, B, was excited, but the result was not so striking as those afterwards obtained owing to misjudging the time at which the response of B would show itself

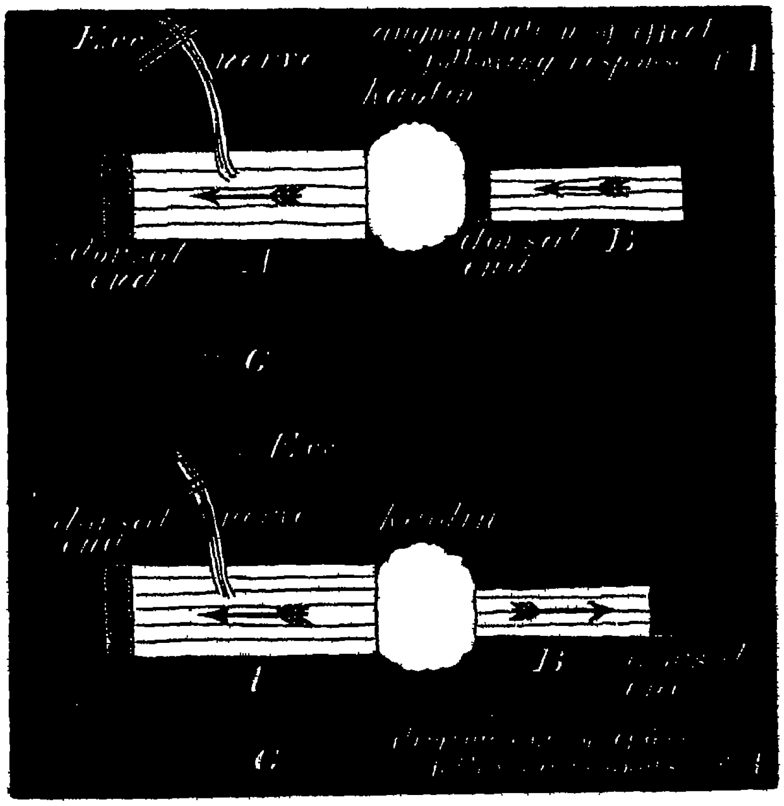
EXPERIMENT 1.—Torpedo 25 × 16 centims Nerve organ preparation A, 20 × 10 × 15 millims. Strip of organ B, 20 × 5 × 5 millims. Second Nerve excited 15 millims. from entry into A by break of K_1.

Nerve organ response of A only to excitation of its nerve.

Period of closure of galvanometer circuit.			
K_2-K_3 01"-0125"	K_2-K_3 0125"-015"	K_2-K_3 015"-0175	K_2-K_3 0175"-02"
G $\frac{1}{10}$ 0	G $\frac{1}{100}$ + 10	G $\frac{1}{100}$ + 365	G $\frac{1}{100}$ + 441

Response of A led through B; B favourable.

	Period of closure of galvanometer circuit			
I	K_2-K_3 0225"-025"	K_2-K_3 ·025"-0275"	K_2-K_3 0275"-03"	K_2-K_3 03"-0325"
Augmentation of response of A	G. $\frac{1}{10}$ + 110	G $\frac{1}{10}$ + 200	G. $\frac{1}{10}$ + 210	G. $\frac{1}{10}$ + 95
II	Response of $\underleftarrow{A}$ led through $\underrightarrow{B}$, B unfavourable			
	G $\frac{1}{10}$ + 180	+ 28	+ 8	+ 30



I
B favourable.

II
B unfavourable

---

* These rheotome readings indicate the time relations of the development of the nerve organ response of A only.

A second similar strip, B′, was now added on to B, and the response of $\underleftarrow{A}$ led through $\underleftarrow{B}$ and $\underleftarrow{B'}$, both favourable, that is, arranged as in I. (this is indicated by the arrows).

	Period of closure of galvanometer circuit.			
	K_2-K_3 ·0225″-·025″	K_2-K_3 ·025″-·0275″	K_2-K_3 ·0275″-·03″	K_2-K_3 ·03″-·0825″
Galv. $\frac{1}{10}$ Augmentation of A		+ 145	+ 130	
Response of $\underleftarrow{A}$ led through $\underrightarrow{B}$ and $\underrightarrow{B'}$; both unfavourable, that is, arranged as in II.				
Diminution of A. Galv $\frac{1}{10}$	+ 80	− 2	+ 9	+ 22

EXPERIMENT 2.—Nerve organ preparation, 30 × 10 × 15, A. Three strips, each 20 × 5 × 5, B_1, B_2, B_3.

Response of nerve organ preparation A only to excitation of its nerve.	Period of closure of galvanometer circuit			
	K_2-K_3 ·01″-·0125″	K_2-K_3 ·0125″-·015″	K_2-K_3 ·015″-·0175″	K_2-K_3 ·0175″-·02″
Galv. $\frac{1}{100}$ . . .	0	+ 305	+ 550	+ 130
Response of $\underleftarrow{A}$ led through $\underleftarrow{B_1}$, $\underleftarrow{B_2}$, $\underleftarrow{B_3}$, all favourable and placed in series				
I	·02″-·0225″	·0225″-·025″	·025″-·0275″	·0275″-·03″
Galv. $\frac{1}{10}$. Augmentation of A	+ 130	+ 459	+ 461	+ 310
II. Response of $\underleftarrow{A}$ led through $\underrightarrow{B_1}$, $\underrightarrow{B_2}$, $\underrightarrow{B_3}$; all unfavourable				
Galv $\frac{1}{10}$ Diminution of A	+ 48	+ 130	+ 238	+ 252

	·0225″-·025″	
Augmentation $\underleftarrow{A}$; $\underleftarrow{B_1}$, $\underleftarrow{B_2}$, $\underleftarrow{B_3}$ favourable, I	+ 515	Galv. $\frac{1}{10}$ shunt
Diminution $\underleftarrow{A}$; $\underrightarrow{B_1}$, $\underrightarrow{B_2}$, $\underrightarrow{B_3}$ unfavourable, II	+ 134	”
Augmentation $\underleftarrow{A}$; $\underleftarrow{B_1}$, $\underleftarrow{B_2}$, $\underleftarrow{B_3}$ favourable, I	+ 380	”
Diminution $\underleftarrow{A}$; $\underrightarrow{B_1}$, $\underrightarrow{B_2}$, $\underrightarrow{B_3}$ unfavourable, II.	+ 52	”

EXPERIMENT 3.—Large Torpedo, 45 × 32 centims. Nerve organ preparation, A, 60 × 30 × 20 millims. Nerve excited 30 millims. from point of entry into A. Temperature 12° C. 3 GROVES in primary, secondary coil at 3000.

RESPONSE of A only.

Galvanometer	Period of closure of galvanometer circuit.			
	K_2-K_3 015″-0175″	K_2-K_3 0175″-02″	K_2-K_3 02″-0225″	K_2-K_3 0225″-025″
$\frac{1}{100}$	0	+ 210	+ 505	+ 232

STRIP of organ prepared 60 × 15 × 12 millims.

Response of A led through B
← ←

Favourable, as in I Galv $\frac{1}{10}$ $K_2 - K_3$ 0275″-·03″		Unfavourable, as in II. Galv $\frac{1}{10}$ $K_2 - K_3$ 0275″-03″	
Augmentation	+ 670	Diminution	+ 51
,,	+ 527	,,	+ 30
,,	+ 501	,,	+ 95
,,	+ 492	,,	+ 145

These experiments show that the electromotive change which is evoked in the nerve organ preparation in response to excitation of its nerve is of sufficient intensity to produce a similar change in another strip through which its current is led. The evidence is in all cases the difference in the readings when this second strip is placed so that its response shall alternately augment and diminish that of the primary nerve organ preparation. It will be noticed that such augmentation and diminution occurs at about 1/100″ after the maximum of the primary nerve organ response has been reached. Now, if the current of the primary response can thus excite an isolated strip of organ, it must much more excite its own tissue, for only a derivation passes through the isolated strip. In this connexion an observation of JOLYET occurred to me, which I state from memory. He noticed in a vigorous fish that his chronograph, which was connected with the end surfaces of the organ columns of a brainless Torpedo, gave, in response to a single excitation of electrical nerves, a wavy fluctuating movement. This he attributed to the fact that, owing to the slow rate of transmission in the electrical nerves of the Torpedo, the excitatory change was probably initiated at different times in different parts of the organ mass. I had myself observed a still more remarkable instance of the same phenomenon.

In making a nerve organ preparation from a vigorous Torpedo, the brain of which had been destroyed. I held a small mass of cut-out organ grasped between the fingers and thumb of my left hand. With the right hand I divided the electrical nerve with a single stroke of a pair of sharp scissors. To my great surprise, I experienced a shock in my left hand which was of a distinctly multiple character. I performed this experiment on three separate occasions, and am now led to think it meant primary, secondary, tertiary, &c., responses. The fact of my not obtaining any evidence of such responses in my previous work would be probably due, first, to the less active condition of the winter fish; secondly, to my not suspecting the existence of, and so not carefully looking for, second and third apices in the electrical curve (a factor of great importance in rheotome work); and, thirdly, to my using a less delicate instrument and too long a period of galvanometer closure. This must explain why I did not then find what I obtained now with great ease, the evidence that the electrical curve of the response of the nerve organ preparation to *single* excitation of its nerve is, in vigorous fish, always multiple in character, the apex of the primary response being followed after an interval of 1/100″ by a second rise, and its apex by a third rise, and so on.

In the following experiments the circuit was arranged as in fig 1, but the secondary coil was not included in the galvanometer circuit, it being connected with a pair of platinum electrodes upon which the nerve of the nerve organ preparation was placed.

EXPERIMENT 1.—Large Torpedo, 48 × 32 centims. A large mass of organ was cut from median edge of left organ, including entry of second electrical nerve. Mass measured 70 × 60 × 15 millims. Nerve excited 20 millims. from point of entry 3 GROVES in primary; secondary coil at 5000. Mass led off by saline kaolin pads on skin surfaces.

Galvanometer	Period of closure of galvanometer circuit.									
	K_2–K_3 ·01″ to 0125″	K_2–K_3 ·0125″ to 015″	K_2–K_3 ·015″ to ·0175″	K_2–K_3 ·0175″ to 02″	K_2–K_3 02″ to ·0225″	K_2–K_3 0225″ to ·025″	K_2–K_3 ·025″ to 0275″	K_2–K_3 0275″ to ·03″	K_2–K_3 ·03″ to ·0325″	K_2–K_3 0325″ to ·035″
$\frac{1}{100}$	0	+ 448	+ ∞ + 95 G. $\frac{1}{1000}$	+ 318	+ 280 + 254	+ 510 + 560	+ 265 + 234	+ 76	+ 70	+ 38

1st apex.
|
Primary response.

2nd apex.
|
Secondary response.

EXPERIMENT 2.—Large Torpedo, 62 × 38 centims. The brain was destroyed, and the whole organ used. The fish was therefore placed on a glass plate, with the ventral skin over the whole organ resting upon a cloth pad moistened with sea-water. A large pad of filter paper moistened with sea-water was applied over the dorsal skin; the non-polarisable electrodes were connected with the two pads. Nerves exposed and excited by Pt wire electrodes 30 millims. from organ. 2 GROVES in primary; secondary coil at 7000. Temperature 10° C.

Galvanometer.	Period of closure of galvanometer circuit.						
	K_2-K_3 01″-015″	K_2-K_3 015″-02″	K_2-K_3 02″-025″	K_2-K_3 025″-03″	K_2-K_3 ·03″-·035″	K_2-K_3 035″-04″	K_2-K_3 04″-045″
$\frac{1}{100}$	0	+ 95	+ 45	+ 30	+ 75	+ 36	+ 10
Repeated	0	+ 61	+ 17	+ 12	+ 70	+ 30	+ 10
,,	0	+ 50	+ 17	+ 8	+ 34	+ 25	+ 10

1st apex.
Primary response.

2nd apex.
Secondary response

Galvanometer.	K_2-K_3 0125″ to 015″	K_2-K_3 015″ to ·0175″	K_2-K_3 0175″ to 02″	K_2-K_3 02″ to ·0225″	K_2-K_3 0225″ to 025″
$\frac{1}{10}$	0	+ 85	+ 170	+ 73	+ 34

1st apex.

K_2-K_3 03″ to 0325″	K_2-K_3 0325″ to 035″	K_2-K_3 ·035″ to ·0375″	K_2-K_3 0375″ to 04″
+ 60 + 55	+ 115 + 120	+ 65	+ 21

2nd apex

EXPERIMENT 3 —A mass of organ, including entry and distribution of second electrical nerve. Led off by saline kaolin pads. Nerve excited 30 millims. from point of entry into organ. 2 GROVES in primary; secondary coil at 7000.

Galvanometer	K_2-K_3 01″ to ·015″	K_2-K_3 015″ to ·02″	K_2-K_3 02″ to 025″	K_2-K_3 025″ to 03″	K_2-K_3 03″ to 035′	K_2-K_3 035″ to 04″	K_2-K_3 04″ to 045″	K_2-K_3 045″ to 05″	K_2-K_3 05″ to 055″
$\frac{1}{100}$	+ 36	+ ∞ G $\frac{1}{1000}$ + 80	+ 255	+ 405	+ 190	+ 265	+ 66	+ 35	+ 18

1st apex — Primary response

2nd apex — Secondary response

3rd apex — Tertiary response

Galvanometer	K_2-K_3 01″ to ·0125″	K_2-K_3 0125″ to 015″	K_2-K_3 015″ to 0175″	K_2-K_3 0175″ to 02″	K_2-K_3 02″ to 0225″	K_2-K_3 0225″ to 025″	K_2-K_3 025″ to 0275″	K_2-K_3 0275″ to 03″	K_2-K_3 03″ to 0325″	K_2-K_3 0325″ to 035″	K_2-K_3 035″ to 0375″	K_2-K_3 0375″ to 04″	K_2-K_3 04″ to 0425″	K_2 K_3 0425″ to ·045′
$\frac{1}{100}$	0	+ 48	+ 367	+ 316	+ 75	+ 120	+ 225	+ 212	+ 89	+ 64	+ 98	+ 130	+ 30	+ 24

Primary response

Secondary response

Tertiary response

EXPERIMENT 4.—Slice of organ including 8 to 10 columns, with second electrical nerve supplying it. Strip measured 65 × 15 × 10 millims. Nerve excited 30 millims. from point of entry. Induction apparatus as in 3.

Galvanometer.	K_2-K_3 0·1″–015″	K_2-K_3 ·015″–02″	K_2-K_3 02″–·025″	K_2-K_3 ·025″–03″	K_2-K_3 03″–·035″	K_2-K_3 ·035″–04″	K_2-K_3 04″–·045″
$\frac{1}{100}$	0	+ ∞ G. $\frac{1}{1000}$ + 75	+ 565	+ 345	+ 330	+ 160	+ 35

This shows no second apex with this galvanometer closure, and is instructive as showing how a long closure, by riding as it were over two wave apices, misses the second rise; a more minute analysis revealed it.

Galvanometer	K_2–K_3 01′ to 0125″	K_2–K_3 0125″ to 015″	K_2–K_3 015″ to 0175″	K_2–K_3 0175″ to 02″	K_2–K_3 02″ to 0225″	K_2–K_3 0225″ to 025″	K_2–K_3 025″ to 0275″	K_2–K_3 0275″ to 03″	K_2''–K_3 03″ to 0325″	K_2–K_3 0325″ to 035″
$\frac{1}{100}$	0	+ 25	+ 460	+ ∞ G $\frac{1}{1000}$ + 65	+ 518	+ 80	+ 88	+ 150	+ 90	
,,	0	+ 15	+ 580	+ ∞	+ 135	+ 84	+ 90	+ 125	+ 95	+ 28

1st apex
|
Primary
response

2nd apex
|
Secondary
response

EXPERIMENT 5.—Torpedo 25 × 16 centims. Nerve organ preparation including 4 or 5 columns only, with second nerve attached. Nerve excited 15 millims. from organ. 3 GROVES in primary; secondary coil at 5000.

K_2–K_3 01″ to 0125″	K_2–K_3 0125″ to 015″	K_2–K_3 015″ to 0175″	K_2–K_3 0175″ to 02″	K_2–K_3 0225″ to 025″	K_2–K_3 025″ to 0275″	K_2–K_3 0275″ to 03″	K_2–K_3 03″ to 0325″	K_2–K_3 0325″ to 035″	K_2–K_3 035″ to 0375″	K_2–K_3 ·0375″ to 04″	K_2–K_3 04″ to 0425″
0	+ 305	+ 550	+ 130	+ 34	+ 80	+ 98	+ 115	+ 125	+ 79	+ 28	+ 14

1st apex
|
Primary
response

Secondary
response.

EXPERIMENT 6.—Torpedo 40 × 29 centims. Nerve organ preparation including 5 or 6 columns, supplied by second nerve. Preparation 35 × 10 × 8 millims. Temperature 15° C. Nerve excited 25 millims. from organ. 3 GROVES in primary; secondary 4000.

Galvanometer.	K_2–K_3 01″ to 0125″	K_2–K_3 0125″ to 015″	K_2–K_3 015″ to ·0175″	K_2–K_3 0175″ to 02″	K_2–K_3 02″ to 0225″	K_2–K_3 0225″ to 025″	K_2–K_3 025″ to 0275′	K_2–K_3 0275″ to 03″	K_2–K_3 ·03″ to 0325″	K_2–K_3 0325″ to 035″
$\frac{1}{100}$	0	+ 190	+ 118	+ 48	+ 106	+ 124	+ 66	+ 24	+ 6	+ trace

Primary.

Secondary

EXPERIMENT 7.—Torpedo 45 × 32 centims. Nerve organ preparation 50 × 10 × 12 millims., containing 5 or 6 columns, supplied by second nerve. Nerve excited 15 millims. from point of entry. 3 GROVES in primary; secondary coil at 5000.

Galvanometer	K_2-K_3 ·01″ to ·0125″	K_1-K_3 0125″ to 015″	K_2-K_3 015″ to 0175″	K_2-K_3 0175″ to 02″	K_2-K_3 ·02″ to 0225″	K_2-K_3 0225″ to 025″	K_2-K_3 025″ to 0275″	K_2-K_3 ·0275″ to 03″	K_2-K_3 03″ to 0325″	K_2-K_3 0325″ to 035″	K_2-K_3 035″ to 0375″
$\frac{1}{100}$	0	+ 175	+ 450	+ 208	+ 60	+ 52	+ 44	+ 45	+ 118	+ 66	+ 16
			Primary.						Secondary.		

These experiments show that not only in the entire fish and in a large mass of organ, but also in a strip containing a few columns, the response to excitation of the nerve is multiple in character. It will be seen that there are some discrepancies in the time interval between the primary and secondary response; it varies from ·01″ to ·015″. This variation is probably connected with the activity of the fish used for experiment. It is not apparently due to temperature. With a rise of temperature the apex of each response moves up towards the zero; that is, they all occur earlier, but at the same interval after one another. To ascertain this, experiments were made with a nerve organ preparation at different temperatures, and the results are shown in the following Tables :—

EXPERIMENT 8.—Torpedo 45 × 32 centims. Nerve organ preparation 60 × 20 × 10 millims. Second nerve excited 30 millims. from point of entry. 2 GROVES in primary; secondary at 3000.

Galvanometer $\frac{1}{100}$	K_2–K_3 ·075″ to ·01″	K_2–K_3 01″ to 0125″	K_2–K_3 0125″ to ·015″	K_2–K_3 015″ to ·0175″	K_2–K_3 0175″ to ·02″	K_2–K_3 02″ to 0225″	K_2–K_3 0225″ to ·025″	K_2–K_3 025″ to 0275″	K_2–K_3 0275″ to 03″	K_2–K_3 03″ to 0325″	K_2–K_3 0325″ to 035″	K_2–K_3 035″ to 0375″	K_2–K_3 0375″ to ·04″	K_2–K_3 04″ to 0425″	K_2–K_3 ·0425″ to 045″	K_2–K_3 045″ to 0475″	K_2–K_3 0475″ to 05″	K_2–K_3 05″ to 0525″	K_2–K_3 0525″ to 055″	K_2–K_3 055″ to ·0575″	K_2–K_3 0575″ to 06″
Temperature 16° C.	0	0	0	0	+ 210	+ 505 1st apex	+ 232	+ 70	+ 138	+ 175 2nd apex	+ 132	+ 85	+ 202 3rd apex	+ 105	+ 20	+ 18	+ 31	+ 84 4th apex	+ 45	+ 12	
Temperature 18° C.		0	+ 51	+ 528 1st apex	+ 421	+ 100	+ 95	+ 138 2nd apex	+ 68	+ 87	+ 164 3rd apex	+ 89	+ 18	+ 11	+ 9	+ 8	+ 120 4th apex	+ 75	+ 20	+ 7	

EXPERIMENT 9.—Torpedo 52 × 37 centims. Nerve organ preparation 60 × 45 × 22 millims. Second nerve excited 30 millims. from point of entry. 3 GROVES in primary; secondary at 5000

Galvanometer $\frac{1}{100}$.	K_2–K_3 ·075″ to ·01″	K_2–K_3 01″ to 0125″	K_2–K_3 0125″ to ·015″	K_2–K_3 015″ to ·0175″	K_2–K_3 0175″ to ·02″	K_2–K_3 02″ to 0225″	K_2–K_3 0225″ to ·025″	K_2–K_3 025″ to 0275″	K_2–K_3 0275″ to 03″	K_2–K_3 03″ to 0325″	K_2–K_3 0325″ to 035″	K_2–K_3 035″ to 0375″	K_2–K_3 0375″ to ·04″	K_2–K_3 04″ to 0425″	K_2–K_3 ·0425″ to 045″	K_2–K_3 045″ to 0475″	K_2–K_3 0475″ to 05″	K_2–K_3 05″ to 0525″	K_2–K_3 0525″ to 055″	K_2–K_3 055″ to ·0575″	K_2–K_3 0575″ to 06″
Temperature 11° C.	0	0	0	0	+ 300	+ 750 1st apex	+ 586	+ 215	+ 251	+ 302 2nd apex	+ 236	+ 254	+ 255 3rd apex	+ 112	+ 40	+ 61 4th apex	+ 60	+ 25	+ 10	+ 4	+ 2
Temperature 15° C.	0	+ 85	+ 472 1st apex	+ 324	+ 146	+ 70	+ 112 2nd apex	+ 79	+ 28	+ 4	+ trace										
Temperature 18° C.	+ 80	+ 546 1st apex	+ 412	+ 123	+ 45 + 397 G. $\frac{1}{10}$	+ 680 G. $\frac{1}{10}$ 2nd apex	+ 615 G. $\frac{1}{10}$	+ 244 G. $\frac{1}{10}$	+ 136 G. $\frac{1}{10}$												

The preparations used in these temperature experiments were made from very vigorous Torpedoes, and, as will be noticed, they give four separate responses to one excitation. The activity of the fish has great influence on the result. Occasionally I obtained from sluggish fish a nerve organ response with a very slight, barely perceptible, secondary effect, only revealed by close rheotome analysis. This was not due to the fact that the primary response was of less intensity, but was evidently dependent upon the diminished excitability of the tissue ; since in excitable tissue obtained from vigorous fish a well-marked secondary response occurred following minimal excitation of the nerve. The following experiment shows a maximal and a minimal effect · the maximal effect has four apices :—

Experiment 10.—Torpedo 46 × 31 centims. Nerve organ preparation 48 × 10 × 20 millims. Nerve excited 40 millims. from point of entry. 3 Groves in primary.

Maximal effect Galv $\frac{1}{100}$. Secondary coil 7000

K_2-K_3 0125″ to ·015″	K_2-K_3 015″ to 0175″	K_2-K_3 0175″ to 02″	K_2-K_3 02″ to 0225″	K_2-K_3 0225″ to 025″	K_2-K_3 025″ to ·0275″	K_2-K_3 0275″ to 03″	K_2-K_3 03″ to ·0325″	K_2-K_3 0325″ to 035″	K_2-K_3 035″ to ·0375″	K_2-K_3 0375″ to 04″	K_2-K_3 04″ to 0425″	K_2-K_3 0425″ to 045″	K_2-K_3 045″ to 0475″
+ 290	+ 494	+ 198	+ 54	+ 85	+ 70	+ 125	+ 131	+ 52	+ 71	+ 151	+ 75	+ 18	+ 10
Minimal effect Galv $\frac{1}{10}$ Secondary coil 30.													
0	+ 900	+ 645	+ 120	+ 80	+ 135	+ 140	+ 75	+ 18					
repeated													
0	+ 850	+ 600	+ 65	+ 80	+ 124	+ 61	+ 10						
Maximal effect Galv. $\frac{1}{100}$ Secondary coil 7000.													
+ 208	+ 435 1st apex	+ 205	+ 69	+ 84 2nd apex	+ 48	+ 125	+ 131 3rd apex	+ 36	+ 84	+ 111 4th apex	+ 62	+ 12	+ 8

The secondary response can be obtained not only in nerve organ preparations when the primary response is evoked by stimulation of the nerve trunk, but also in the strip of organ when the primary response is evoked, as described in Part I., by the passages of an induction shock through the strip. It is, however, more difficult to obtain it in this latter case. It is always obtained with ease when the strip is so prepared as to include the trunk of a nerve supplying it. Since, in this case, the strip becomes in reality an ordinary nerve organ preparation with a very short nerve, it is probable that the difficulty of obtaining it in carefully selected strips containing no obvious nerve trunk is connected with the risk of injury attending the preparation of such strips. Since, however, every such preparation becomes in reality a nerve organ preparation, it is clear that if the preparation is a good one it must occur. The following is an instance of its occurrence in a strip of organ containing no obvious nerve bundles :—

EXPERIMENT 11.—Torpedo 52 × 37 centims Strip of organ 60 × 8 × 8. 3 GROVES in primary; secondary coil 5000. Strip excited by passage through its length of an induction shock, as in Part I. Circuit arranged as in fig. 1.

Direction of Induction Shock (+).											
Galv $\frac{1}{100}$						Galv $\frac{1}{10}$					
K_2-K_3 0" to 0025"	K_2-K_3 0025" to 005"	K_2-K_3 005" to ·0075"	K_2-K_3 0075" to ·01"	K_2-K_3 01" to ·0125"	K_2-K_3 ·0125" to 015"	K_2-K_3 015" to 0175"	K_2-K_3 0175" to ·02"	K_2-K_3 02" to 0225"	K_2 K_3 0225" to 025"	K_2-K_3 025" to 0275"	K_2-K_3 0275" to 03"
+ 446 Induction shock	+ 12	+ 50	+ 342 Primary response	+ 218	+ 70	+ 243	+ 305 Secondary response	+ 154	+ 54		
Direction of Induction Shock (−)											
− 449 Induction shock	− 6	+ 24	+ 215 Primary response	+ 132	+ 55	+ 271 + 231	+ 375 + 409 Secondary response	+ 257 + 274	+ 88 + 109	+ 62 + 69	+ 41

The experiment shows that the secondary response attains its maximum 1/100" after that of the primary, and that it is independent of the direction of the exciting induction shock.

In all the preceding experiments the second apex occurs at about 1/100" after that of the primary response. This fact, together with the fact that the current of the primary response itself excites a strip when led through it, justifies the conclusion that the second rise is a true secondary response excited by the rise of the primary; but, as the tissue when excited by an induction shock has been shown in Part I. to attain the maximum of its response in rather less than 1/100", it seemed advisable to devise an experiment which would clearly demonstrate that this second rise noticed in all the preceding experiments is unquestionably an excitation evoked by the current of the primary response. This is proved by the following experiment, in which all the information previously gained was made use of in order to obtain *both* the secondary response in a nerve organ preparation *and* the independent response of an isolated strip to the passage through it of the current of the primary response. There can be no question that the difference in the galvanometric readings obtained by leading the current of the nerve organ preparation through an interposed strip (as in the first experiments of Part II.), when this is placed so that its own response may first coincide with and then oppose that of the nerve organ preparation, is due to the fact that the second interposed strip is excited by the led-through current of the nerve organ response. If, then, the character of this response, apart from the interposed strip, be such that it shows a secondary rise, and the time relations of this rise agree with those of the augmentation and diminution found when the strip is interposed, then we have conclusive evidence that this secondary rise, even though it may begin later after the primary than might be expected, is a true secondary response in the sense that it is caused by the excitation of the nerve organ tissue by the passage through its substance of the current of its own primary response.

The following experiment will make this clear ·—

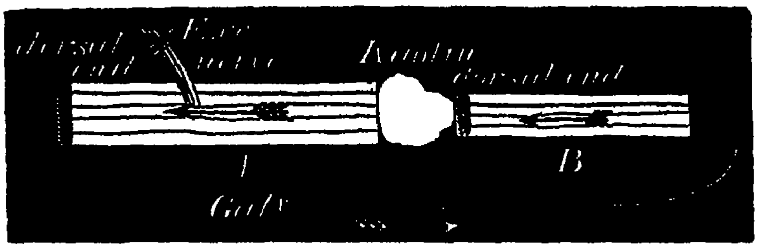
EXPERIMENT 12.—(Selected out of three sets of experiments.) Large Torpedo, 52 × 37 centims. Mass of organ A, measuring 60 × 45 × 22, including entry of second nerve. Nerve excited 30 millims. from entry into organ. Three GROVES in primary; secondary coil at 5000.

Time relations of excitatory response of $\underset{\longleftarrow}{\text{A}}$ only; Galv $\frac{1}{100}$

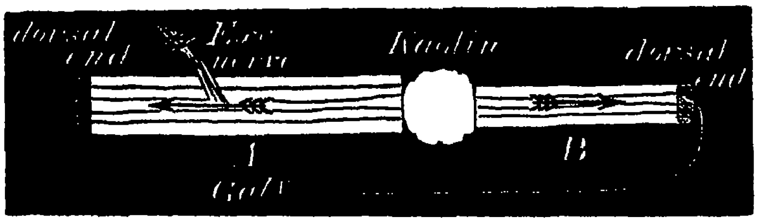
K_2–K_3 015″ to 0175″	K_2–K_3 0175″ to ·02″	K_2–K_3 02″ to 0225″	K_2–K_3 0225″ to 025″	K_2–K_3 025″ to ·0275″	K_2·K_3 0275″ to 03″	K_2–K_3 03″ to 0325″	K_2–K_3 0325″ to 035″	K_2–K_3 ·035″ to ·0375″	K_2 K_3 0375″ to 04″	K_2–K_3 04″ to ·0425″	K_2–K_3 0425″ to 045″
0	+ 380	+ 750 1st apex	+ 586	+ 215	+ 251	+ 302 2nd apex	+ 236	+ 254	+ 255 3rd apex	+ 112	+ 40
Strip of organ B prepared 60 × 8 × 10 millims, and interposed between A and galvanometer.											
I. Time relations of response of $\underset{\longleftarrow}{\text{A}}$ with $\underset{\longleftarrow}{\text{B}}$ interposed favourable; Galv. $\frac{1}{100}$.											
0	+ 105	+ 295	+ 275	+ 86	+ 160 Au	+ 166 gmentati	+ 162 on	+ 133	+ 170	+ 102	+ 26
II. Time relations of response of $\underset{\longleftarrow}{\text{A}}$ with $\underset{\longrightarrow}{\text{B}}$ interposed unfavourable; Galv $\frac{1}{100}$											
				+ 90	+ 106 D	+ 94 iminutio	+ 75 n	+ 92	+ 161	+ 91	
I repeated Response of $\underset{\longleftarrow}{\text{A}}$ with $\underset{\longleftarrow}{\text{B}}$ favourable; Galv. $\frac{1}{100}$											
				+ 84	+ 141 Au	+ 172 gmentati	+ 160 on	+ 158	+ 160	+ 98	+ 76
II. repeated. Response of $\underset{\longleftarrow}{\text{A}}$ with $\underset{\longrightarrow}{\text{B}}$ unfavourable; Galv. $\frac{1}{100}$.											
				+ 71	+ 83 D	+ 76 iminutio	+ 68 n	+ 85	+ 135	+ 42	

The comparison is made between the effect when the nerve organ preparation A alone was led off by its skin ends, and that produced when the leading off occurred at one end through B arranged as shown in I and II. .—

I



II.



The experiment shows that the response of the strip B, as indicated by the augmentation and diminution due to algebraic summation of electrical effects, begins at about ·03″ and attains its maximum during the period of closure, ·03″–·0325″, which is also the period when the secondary rise of the nerve organ preparation only attains its maximum. I therefore conclude that the secondary rise in the electrical excitatory curve (see Plate 52) is due to a second state of excitation evoked in the nerve organ tissue by the current of the primary response, and, if there is a tertiary, that this is similarly caused by the secondary, and so on.

General Conclusions.

(1.) It has been shown by the experiments of which details have been given in Part 1 that an isolated strip of electrical organ containing a few columns with no large nerve trunk entering them may be excited by the passage through the columns of an electrical current of considerable intensity (such as an induction shock) The response of such a strip of organ resembles in all particulars that of a nerve organ preparation evoked by stimulation of the trunk of the nerve supplying it.

(2) From this it follows that the phenomena of "irreciprocal conduction," to which attention has been drawn by du Bois-Reymond, are observed only when the galvanometric effect of the exciting induction shock and that of the response are blended.

(3.) Beyond this apparent irreciprocal conduction, which has been shown to be, in these experiments at least, nothing but algebraic summation of two electromotive effects, there is no evidence of any irreciprocity, the induction shocks, when care is taken to exclude all succeeding electromotive changes from the galvanometer, present no inequality dependent on their being "homodromous" or "heterodromous" in direction.

(4) It has been further shown that a strip of organ can be excited by the passage through its columns of the current due to the response of a nerve organ preparation to stimulation of its nerve.

(5) Finally, it is shown that the excitatory process in the organ of vigorous fish, whether evoked by stimulation of a nerve trunk or by the passage of an induced current through the organ itself, will itself evoke a second excitatory change; this a third, and so on The second change is found to be in all probability a secondary response due to excitation of the nerves of the responding tissue by the current involved in the primary state of excitation. The tissue thus reverberates, and the curve indicating the nature and time relations of an excitatory response must be modified, as shown in Plate 52.

In conclusion, it may be well to refer to some remarks of DU BOIS-REYMOND on the teleological significance of the phenomena of "irreciprocal conduction." He considers that these phenomena to some extent solve the puzzle as to how the organ is insulated It is not insulated, he says, but irreciprocal conduction performs a function similar to insulation. Thus, "the arrangement which does really exist is superior even to the insulating property of the cover of the individual columns, for such a property would indeed oblige the currents, between points of the lateral surfaces of all the columns, to take their route along the column, but it would present no obstacle to the return of the currents from the dorsal to the ventral surface by the shortest route, through the neighbouring columns" And further on .—"However that may be, the instance of internal adaptation to which we have been now led far surpasses all earlier ones in ingenuity It would certainly have demanded the profoundest reflection of a clever brain to hit upon the idea of making each column as good a conductor for its own shock as any other animal tissue can be, but comparatively a non-conductor for the current of all other columns. In connexion with the extremely transitory nature of the shock, it is not a little remarkable that it is only currents of extremely short duration that the organ conducts irreciprocally. Of what service would it have been to the fish if it had become a perfect non-conductor for continuous heterodromous currents also?" *

As a matter of fact, however, each column conducts with equal facility its own homodromous shock and the returning heterodromous current of the shock of its neighbours, but in the latter case it is excited, as indeed it is by the current of its own response. The teleological significance, then, of the phenomena is not what DU BOIS-REYMOND imagines; if anything, it means that a single response has a reverberating character, due probably to the current of the response acting as a stimulus to the nerves in the columns, and thus each column reinforces by its echoes the effect of the primary explosion.

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* DU BOIS-REYMOND, 'Archiv Anat. Physiol. (Physiol. Abtheilg.),' 1887, pp. 102, 104; see also, 'Biological Memoirs,' edited by J. BURDON SANDERSON, 1887. pp. 533, 534

DESCRIPTION OF PLATES.

Plate 51. Electromotive change in an isolated strip of electrical organ following the passage lengthwise through its columns of an induction current. The ordinates represent scale readings of the galvanometer deflection, the abscissæ denote the time after the passage of the induction shock which occurs at zero.

The first electromotive effect is that due to the induction current itself, and is shaded black, the black line is prolonged upwards rather indefinitely, since its apex cannot strictly be compared with the height of the subsequent excitatory change, as owing to its rapidity it fails to give a proportionate galvanometric effect.

Fig 1 represents the change following a (+) homodromous induction shock in a strip of organ at temperature 15° C.

Fig. 2 represents the same at temperature 3° C., showing the separation of the response from the induction current.

Fig 3 represents the same change with a (—) heterodromous induction shock at 15° C.

Fig. 4, the same at 3° C.

Plate 52 Electromotive change following a single excitation of nerve trunk of a nerve organ preparation in vigorous summer Torpedoes.

Fig. 1 shows the change in two distinct preparations at 15° C The smaller one shows a primary (i.), followed by a secondary response (ii.); the larger shows also a tertiary.

Fig. 2 shows the change in two vigorous fish at low temperatures, 10° C, both show four responses, I, II., III., IV., following the single excitation of the nerve.

XIII *The Early Development of the Pericardium, Diaphragm, and Great Veins.*

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[PLATES 53–61.]

THE following investigation was begun three years ago with a view to inquire into the development of the pericardium, but it transpired that this question is inseparable from that of the development of the heart, great veins, and diaphragm. Since the Avian pericardium is complicated by various septa whose exact nature is not generally agreed upon,* the embryos of Mammals, especially of Rabbits, have been used for the investigation, and Human embryos have been obtained to illustrate some of the later stages. But, as the embryo of the Rabbit is capricious in its development, it is hardly possible to say upon any particular day after impregnation what stage the embryos may have attained. As a rule, the various members of a litter differ amongst themselves, some being more advanced than others; so that, without this qualification, it would be misleading to specify, as some authors have done, the exact age of the embryo described or depicted.

The origin of the Mammalian heart has been elucidated by various observers, especially by BALFOUR,† HENSEN,‡ HIS,§ and KOLLIKER,|| and only requires to be mentioned so far as it bears upon the present inquiry In the Rabbit the organ begins to develop during the first half of the eighth day. And its commencement is indicated by a slight bending of the splanchnopleure into the widely separated halves of the cœlom (fig. 1, *Ht.*). This loop is thicker than the rest of the splanchnopleure,

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* HUXLEY, "On the Respiratory Organs of the Apteryx," 'Zool. Soc. Proc.,' 1882, p. 560

† 'A Treatise on Comparative Embryology,' by FRANCIS M BALFOUR, London, 1885, vol. 2, p. 633

‡ "Beobachtungen uber die Befruchtung und Entwicklung des Kaninchens und Meerschweinchens," v. HENSEN, 'Zeitschrift fur Anatomie und Entwicklungsgeschichte,' 1876, p. 344

§ "Mittheilungen zur Embryologie der Säugethiere und des Menschen," W HIS, 'Archiv für Anatomie und Physiologie,' 1881, pp. 302 *et seq*; also 'Anatomie Menschlicher Embryonen,' Leipzig, vols 1, 2, and 3, and plates.

|| 'Entwicklungsgeschichte des Menschen und der Hoheren Thiere,' Leipzig, 1879, p 289.

owing to multiplication and elongation of its cells. At this time the portion of the cœlom into which the cardiac loops project is more capacious than the rest, but has not the same lateral extension. Its somatopleure, after running a little way outwards, turns abruptly ventralwards to join the splanchnopleure. At the foremost end of the rudimentary heart, where the bending of the somatopleure is greatest, both membranes disassociate themselves at an early period from the peripheral uncleft mesoblast; but further back they retain their original connexions. The accompanying drawing was made from a section which was slightly oblique, and illustrates both of these points (fig. 1). Afterwards, as development proceeds, the whole of the cardiocephalic region ultimately frees itself in this way from the peripheral uncleft mesoblast.

The splanchnic cardiac loops grow rapidly during the eighth day, and each acquires an endothelial lining. The latter, as BALFOUR points out, is derived from the splanchnic mesoblast, and cells of a similar nature reach inwards towards the notochord, and are concerned in the formation of the dorsal aortæ. The endothelial linings form a continuous ring, although the splanchnic cardiac loops are incomplete ventralwards (fig. 2, *Ht.*). As the pharynx closes in, the separate halves of the heart gradually approximate (fig 3, *Ht.*), and finally unite at the ventral aspect of the alimentary canal. When this is completed the heart remains for a time attached to the pharynx by the mesocardium posterius, and to the ventral wall of the cœlom by the mesocardium anterius. From the fore end of the heart the aortæ pass round the pharynx to join the dorsal aortæ, which, although distinctly formed, have not as yet coalesced During the first half of the eighth day the aortæ are the only vessels which leave or enter the heart, but afterwards the vitelline veins develop and exercise an important influence upon the development of the pericardium. The specimens in my possession (fig. 3) do not seem to favour the view that the cardiac loops become complete tubes before their union*; it seems as if their concavities merely come together and unite; but, of course, the endothelial linings must be excepted from this statement. Moreover, as the halves of the heart join together the continuity of the hypoblast between them is broken, and its epithelium takes no part in the formation of the organ. Hence it follows that the hypoblast which lines the pharynx ceases to unite with that which clothes the ventral aspect of the cardiac cœlom by passing through the heart or mesocardia.

The effect of these changes upon the cardiac cœlom is comparatively simple. As the splanchnopleure closes in to form the pharynx the separate halves of the cœlom come together, but are, at first, partitioned from one another by the mesocardium posterius and anterius, with the heart in their midst; and thus a ventral mesentery originates which is attached to the pharynx and supports the heart.

By the beginning of the ninth day the mesocardium anterius has disappeared, with the exception of a small remnant which persists for some days, and the halves of the cardiac cœlom coalesce to form a single chamber. The foremost portion of the heart, owing, presumably, to the shortness of the supracardiac splanchnopleure, has a wide attachment to the pharynx, but the mesocardium posterius forms a thin support for the venous end (figs. 15B and 16B). By this time, moreover, the vitelline veins have appeared, and run inwards from the vascular area, at right angles to the axis of the embryo, to enter the heart (fig. 4, *Vit. V.*). These vessels begin in the vascular area by means of a venous mesh-work,[*] and reach the heart by way of the splanchnopleure, and, consequently, by passing across the ventral boundary of the cœlom. As their passage is at right angles to the axis of the embryo, they form a demarcation between the cardiac and pleuro-peritoneal portions of that space This may be proved by longitudinal sections of embryos of the beginning of the ninth day, which, uncut and slightly magnified, have the appearances shown in the accompanying figure (fig. 4). The sections show that on each side of the pharynx the cœlom is continuous at the dorsal aspect of the vitelline veins (figs 10A, 11A, *Vit. V* , and fig 5, *Vit V.*); and that the part of it in front of those vessels contains the heart, although that behind is, as yet, unoccupied by either lungs or abdominal viscera.

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* BALFOUR, 'Elements of Embryology,' vol. 2, p. 633.

Towards the lateral limits of the embryo, the vitelline veins lie at the foremost end of the pleuro-peritoneal space, and the mesoblast in front of them is uncleft, because, as I have pointed out, the cardiac cœlom does not extend so far outwards (figs 7A and 8A and *Vit V.* and *Blas.*, and 9A, *Vit V.*). In consequence of this, the vein is situated at the junction of the somatopleure and splanchnopleure, and might, not unreasonably, have been thought to unite them. This junction is that which KOLLIKER[†] has named "mesocardium laterale ;" but, inasmuch as it does not, in the earliest stages, form a mesentery for the heart, this term does not seem entirely appropriate ; at later stages this objection disappears, and, as the name is well known, it deserves to be retained.

In future I propose to call the passage by which the cardiac and pleuro-peritoneal portions of the cœlom communicate the "iter venosum," because the great veins have so much to do with its formation, and subsequently with its closure. Its presence has been recognised by HIS[‡] and USKOW[§] both in Rabbits and Human embryos The former author seems reluctant to look upon the pericardium as essentially a portion of the cœlom, and considers that which I have called the iter to have two parts, which he calls the "recessus parietalis" and "recessus abdominalis" respectively These names are only applicable, however, to those portions of the cardiac and pleuro-peritoneal cœlom which, at later stages, lead towards the heart. When the lungs develop they protrude into the recessus abdominalis, so that it has also been called by **His** the recessus pulmonalis[*] Further, it can easily be perceived that the iter venosum corresponds to the passage which in many Vertebrates, especially the Skate and Dog-fish, unites the pericardium with the rest of the body cavity, and whose origin, **Balfour** says, has not been satisfactorily worked out[†] It may be inferred from the foregoing that the iter venosum is bounded ventralwards by the vitelline vein, dorsalwards by the body wall, externally by the mesocardium laterale, and internally by the splanchnopleure, where that membrane is closing in behind the venous end of the heart to form the fore-gut and mesocardium posterius (figs. 16B and 20C, *It. V.*). Behind the heart and vitelline veins the splanchnopleure has not as yet infolded to form the alimentary canal, but runs outwards on either side to unite with the somatopleure (figs. 17B and 18B, *Spl.*). Longitudinal sections near the axis of the embryo and internal to the iter show the heart in its relation to the pharynx (figs. 13A and 14A), and their appearances have been rendered familiar by **Kolliker**,[‡] **Uskow**, and others. Taken alone, they suggest that the heart lies in a separate and distinct chamber of its own; but such an idea is shown to be erroneous, both by earlier embryos and by the other sections through the iter. The appearance seems due to the fact that in the cardiac region the halves of the cœlom have already coalesced, whilst behind they are still apart; so that, in consequence, the splanchnopleure which spreads outwards from one to the other envelops the venous end of the heart (fig. 14A), and thus seems to form a closed chamber for it.

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[*] "Recherches sur la formation des annexes fœtales chez les Mammifères" E VAN BENEDEN and C JULIN, 'Archives de Biologie,' vol 5, 1884, p 381

[†] "Entwicklungsgeschichte,' p 295 (figs. 214 and 217).

[‡] HIS, "Mittheilungen zur Embryologie der Saugethiere," 'Archiv für Anatomie und Entwicklungsgeschichte,' 1881, p. 303.

[§] USKOW, "Ueber die Entwicklung des Zwerchfells, des Pericardiums und des Cœloms." 'Archiv f. Anat. und Physiol,' vol 12, 1883, pp. 143 *et seq*

Soon after the heart has become an unpaired organ the ventral wall of the cardiac chamber alters so much that the share the splanchnopleure has in its formation is less obvious. It seems reasonable to infer that, inasmuch as its ventral boundary wall is covered with hypoblast, therefore it is of splanchnic origin, and this is borne out by the younger embryos (figs. 1 to 3, *Hy.*). In longitudinal sections, as **Van Beneden** and **Julin** also show, the hypoblast extends forwards over the ventral wall of the cardiac cœlom to form, with the epiblast, the pro-amnion (fig. 5, *P. am.*).

Authorities are agreed that the mesocardium laterale plays an important part in the development of the pericardium, but some of its features, I think, require further elucidation. Its formation seems to be exceedingly constant in the vertebrate series, and it is recognised to be a junction of splanchnopleure to somatopleure, which serves for the transmission of the somatic venous system into the splanchnic. The former would, in the earlier stages of development, comprise the umbilical veins, the cardinal veins, and the Cuvierian ducts; the latter the vitelline veins and heart.

The question arises whether, as **Kolliker**[§] and **Balfour**[‖] seem to think, the mesocardium laterale is an actual adhesion of the somatopleure to the splanchnopleure, or whether it is a place at which the mesoblast has never separated into those layers. Studied in some transverse sections, and, perhaps, at rather later stages, it seems to possess the characters of an adhesion, and it may in some types, Birds for instance, be of that nature, but in the Rabbit, as we have already seen, it is the place at which the cleft mesoblast gives place to that which is uncleft (*M.L*, figs. 7A and 8A and 9A). The exact position of the mesocardium laterale in a series of sections is marked by the passage of the somatic veins into the splanchnic, and in the embryo which has been figured a vein, which will presently be identified as the umbilical, runs forwards in the somatopleure to empty into the vitelline (fig. 8A, *U.V.*). As I have just remarked, the mesocardium laterale has the appearances of an adhesion in transverse sections (figs. 16B and 21C *M.L.*); but, nevertheless, even transverse sections bear out the previous statements.

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[*] 'Anatomie Menschlicher Embryonen,' pt. 3, p. 146

[†] 'Comp Embryol.' vol. 2, p 628.

[‡] *Loc. cit*, pp. 407 *et seq.*

[§] *Loc. cit.*, p. 295.

[‖] *Loc. cit.*, vol. 2, p. 627.

Various opinions prevail as to the identity of the vein which passes through the mesocardium laterale. KOLLIKER* and USKOW † call it the jugular,‡ whilst BALFOUR speaks of it as being the Cuvierian duct. Neither of these alternatives holds good in the Rabbit's embryo, because the vein which their mesocardium laterale transmits runs from the tail end forwards in the side body wall (fig. 8A, *U.V.*, also figs 16B, 17B, and 18B, *U.V.*), and, therefore, corresponds neither to the jugular vein nor to the Cuvierian duct. At first (early part of ninth day in Rabbit) the anterior cardinal or jugular veins are merely represented by isolated venous spaces by the side of the brain (fig. 15B, *J.V.*), and the posterior cardinals by similar spaces near the Wolffian ducts and tubules (fig. 18B, *P.C.V.*). However, in addition to these, at the level of the mesocardium laterale the body wall contains on each side a spacious vessel, the umbilical, or parietal, vein. These paired vessels run tailwards in the body wall (fig. 18B, *U V*), until they reach the level of the posterior neurenteric canal, where they turn dorsalwards in a portion of the body wall which is continuous with the tail fold of the amnion (fig. 19B, *U.V.*), and in which they communicate with one another, and, as will be described, obtain a connexion with the endometrium.

The umbilical veins develop after the mesocardium laterale, and sooner upon one side of the embryo than upon the other. At the beginning of the ninth day the mesocardium laterale exists on both sides, although only one umbilical vein may have developed, and that partially, as happens to have been the case in one of the embryos depicted (fig. 8A, *U.V.*). Moreover, those vessels do not both acquire a passage towards the heart at the same moment, for sometimes, although each is present, only one may open into the vitelline vein, whilst the other is still separated from it by a thin partition (compare fig. 16B with fig. 17B, *U.V.*). At first the umbilical veins only reach as far forwards as the mesocardium laterale, but later they extend a little further towards the head (seven sections in Series B.), and, as, will be seen later, their foremost part receives the anterior cardinal or jugular veins when those vessels are more fully developed. The portions of the vitelline veins into which the umbilical veins empty themselves cross the ventral boundary of the iter venosum, and, after uniting with each other behind the heart, open together into the venous end of that organ (figs. 14A and 21C, *Vit. V.* and *S.R.*). During the early hours of the ninth day the capacity of these portions of the vitelline veins increases rapidly, and at the same time their connexions by means of the mesocardium laterale and posterius with the body wall and pharynx become more substantial (fig. 20C). Being held by these attachments, the vitelline veins prevent the expansion of the part of the cœlom at their dorsal aspect, and it remains in consequence a narrow passage, the iter venosum. The expanded portion of the vitelline veins may be identified as an early stage of the chamber which HIS * has named the sinus reuniens, and which, after its formation, becomes the ventral boundary of the iter venosum. After these events the iter venosum is by far the narrowest part of the cœlom, and forms a decided constriction between its cardiac and pleuro-peritoneal portions; and, in addition, the septum transversum, or primitive diaphragm, has originated in the following manner:—At the beginning of the ninth day the splanchnopleure, after being attached to the ventral wall of the vitelline vein, is prolonged forwards over the heart without exhibiting any particular bend ventralwards (figs. 9A, 10A, and 11A, *Spl.*). But in embryos of nine days and four hours that membrane, and the hypoblast which covers it, makes a decided bulge where it clothes the ventral aspect of the heart, and is sharply retroflected behind that organ (fig. 5, *Spl.*). This is caused by several circumstances. The expansion and growth of the heart is one of the chief, causing the splanchnopleure, or as this part of it is sometimes called, the cardiopleure, to bulge at its ventral aspect, but the effect of this is limited, and cannot alter the position of that part of the membrane which is continuous with the vitelline veins, or, as they may now be called, the sinus reuniens. This, owing to the attachments of the vitelline veins to the dorsal body wall and pharynx, by means of the mesocardium posterius and laterale, cannot undergo displacement, and, obviously, its fixation is exactly opposite the iter venosum (fig. 5, *It. V.*). The formation of the cranial flexure has also an influence upon the early development of the septum transversum, for it carries no inconsiderable part of the heart and splanchnopleure tailwards beneath the vitelline veins. Another feature of this splanchnic retroflexion is that it stretches across the axis of the embryo from one mesocardium laterale to the other; although, at this stage of the development of the cardio-cephalic region, its mesoblast still passes beyond those limits to become continuous with the peripheral uncleft mesoblast (fig. 22C, *P.M.*). Thus a transverse septum is formed from the splanchnopleure, the anterior surface of which is concave, and supports the heart and gives attachment to the remains of the mesocardium anterius and posterius; whilst its hinder surface, prior to the development of the liver or closure of the alimentary canal, protrudes into the capacious mouth of the vitelline duct (fig. 5, *S.T.*). Most authors have described the septum transversum after the liver has developed, and, therefore, the splanchnic retroflexion which has just been described only resembles the "septum transversum" of HIS,* or the "cloison transversale" of CADIAT,† or the "massa transversa" of USKOW,‡ in its relations to the heart and sinus reuniens. However, its identity and more permanent characters will be evident after the liver has developed.

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* 'Entwicklungsgeschichte,' p. 296, fig. 215.

† USKOW, *loc cit*, p. 167

‡ In these pages the term "jugular vein" is considered as being synonymous with "anterior cardinal vein."

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* HIS, 'Anatomie Menschlicher Embryonen,' part 3, p. 144.

In the Rabbit, and probably in other Mammals, the liver develops upon the hinder surface of the septum transversum. A thickening of the hypoblast and mesoblast on either side of the alimentary canal, and opposite the iter venosum, and close to the ventral wall of the vitelline vein, indicates its commencement (*H. Hy.*, fig. 5, and *L.*, fig. 6). The median part of the septum does not at first participate, but subsequently its cells grow larger, like the rest, and multiply and dispose themselves irregularly in the thickened mesoblast (fig. 22C) and, at the same time, vascular channels appear which acquire openings into the lumens of the vitelline veins. Thus, at its commencement the liver seems to be, in a degree, a bilateral development. After their formation, the liver and septum transversum increase rather rapidly, and the mesocardium laterale becomes thicker (*L.* and *M. L.*, fig. 6). The anterior cardinal veins also develop more completely at this stage (*A. C. V.*, fig. 6), and run along the body wall, past the iter venosum, to empty into the umbilical veins, just before the latter pass through the mesocardium laterale on their way into the sinus reuniens, whose capacity has also increased. The venous spaces which represent the posterior cardinal veins have not, as yet, acquired a passage into the heart. During these events the liver continues to grow upon the septum transversum (*L.*, fig. 24D, also *L.*, fig. 36), until it becomes an organ of some size situated behind the heart and upon the ventral wall of the vitelline veins and sinus reuniens (*L.*, fig. 32E). A number of solid villous processes are associated with its growth, and by their union help to form its substance; others may be observed which, like pseudopodia, project from the ventral wall of the pericardium (fig. 36, *Vil. P.*); these, however, disappear without, as far as can be seen, performing any function. By the eleventh day the septum transversum has become the ventral part of the diaphragm (fig. 42F and 43F, *S. T.*), and a little later, both in Rabbits and Human embryos, its appearances are quite familiar (*V. D.*, fig. 53, also fig. 54H). Soon after the commencement of the liver the somatopleure and splanchnopleure infold in the usual manner, and as the former wraps round the liver it unites on either side with its substance (figs. 24D and 44F). As the splanchnopleure infolds it forms a dorsal mesentery, which supports the gut (fig. 23D, *Mes. D*), and a ventral mesentery, which unites the foremost part of its ventral edge to the liver (fig. 24D, *Mes. D.*) A portion of the latter persists as the gastro-hepatic ligament, or lesser omentum, the remainder disappears, although until the twelfth day it is continuous with the blastoderm, and is the route by which the vitelline veins enter. The last-named vessels, after the splanchnopleure has infolded, run forwards by the side of the alimentary canal, at the dorsal surface of the liver and septum transversum (*Vit. V*, fig. 24D and 25D), as far as the mesocardium laterale, where they receive the umbilical veins and become the sinus reuniens (fig. 26D). The cardiac ends of the umbilical veins are at first unaffected by the infolding of the body wall, but whilst that event is progressing the part of the body wall in which they commence becomes converted into the fœtal part of the placenta.

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* 'Anatomie Menschlicher Embryonen,' vol. 1, p. 125.

† "Du Développement de la Portion Céphalo-Thoracique de l'Embryon, &c.," 'Journal de l'Anatomie et de la Physiologie,' vol. 14, 1878, p. 6

‡ *Loc. cit.*, p. 171.

We have already seen that at the beginning of the ninth day the umbilical veins commence in a portion of the body wall which is continuous with the tail fold of the amnion (fig. 19B); by the middle of the same day the body wall in this region has grown thicker and has still retained its vascularity (figs. 26D, 27D, and 28D), and by the end of the ninth day these changes have advanced further, and there are indications that the portion of the body wall in which they are in progress is being constricted from the rest to become the fœtal placenta (fig. 31, *Plac*). This placental region of the embryo has never wholly separated from the endometrium, although the position of the embryo with regard to the uterine wall has completely changed. During the eighth day the dorsum of the embryo, covered with epiblast, lies in contact with the uterine wall (figs. 1 and 4). The position is the same at the beginning of the ninth day, except that the embryo has parted a short distance from the uterine wall, from which it is partially separated by the folds of the amnion (fig. 14A, also figs. 15B and 16B). Later, the cranial flexure carries the cardio-cephalic region and pro-amnion ventralwards into the interior of the blastodermic vesicle (figs. 5 and 6), and after a while that bend increases so much that the head and tail ends nearly meet (fig. 32E). Whilst these movements are proceeding the embryo turns over upon its right side, carrying the amnion with it (fig. 24D and fig. 31), and its right side then lies upon the uterine wall; and in the placental region this rotation is so complete that its venter is completely turned towards the uterus (figs. 27D and 28D, also fig. 30). Also, in that region, the body wall seems never to entirely dissociate itself from the endometrium, or from the rest of the blastoderm.

Thus, the commencements of the umbilical veins acquire their connexion with the uterine wall without the aid of an allantois. I do not propose at present to consider the development of that organ; but I am unable to confirm the late Professor BALFOUR's statement that the allantois of the Rabbit is formed the same way as in Birds*; nor do KÖLLIKER's observations seem to convey a clearer impression of the actual processes of development. Most authors adopt the views of VON BISCHOFF,* who speaks of and depicts the allantois as a vesicular protrusion which, he says, grows towards and adheres to the uterine wall † The placental stalk of the Rabbit's embryo has at the twelfth day the appearances which VON BISCHOFF describes and depicts, but it bends to the right, not because of its own movements, but because of the rotation of the embryo, nor does it protrude or grow towards the uterine wall. It is true that at the middle of the ninth day the lumen of the hind gut extends into the fœtal placenta (compare figs. 29D, 28D, and 27D, *All.*), but other specimens suggest that this extension, which corresponds to the allantois of other types, is formed by inclusion and not by protrusion (fig. 30, *All.*), and this circumstance throws light upon the pathology of ectopia vesicæ. Moreover, the splanchnopleure itself seems to take no part in the development of the placenta, for the placental and caudal portions of the Rabbit's embryo develop in the space which there is between that membrane and the uterine wall, the latter being covered with the subzonal membrane (*Spl.*, fig. 14A, also figs. 30 and 31).

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* 'Comparative Embryology,' vol. 2, p 281.

The further progress of the heart and venous system and the appearance of an air-breathing apparatus tend to the development of the pericardium and permanent diaphragm. One of the most important events is the formation of the ductus Cuvieri, and their subsequent conversion into the superior venæ cavæ. The history of the somatic venous system has been followed until it comprises an umbilical and a jugular vein on either side, which coalesce in the body wall opposite the mesocardium laterale, through which they pass to empty into the sinus reuniens. As the Wolffian duct and tubules grow (second half of the ninth day) the posterior cardinals undergo further development, and run forwards and empty into the jugulars, just before the latter cross the iter venosum (figs. 33E and 34E, *P. C. V.*). This converts a portion of each of the jugular veins into the ductus Cuvieri, which still pursue the original course of the jugulars through the body wall, and past the iter (figs. 33E and 36, *C. D.*, also fig. 6, *A. C. V.*). Afterwards (second half of tenth day) the growth of the head and of the primitive kidneys and vertebræ is rapid, and in consequence the ductus Cuvieri, which return the blood from both regions, expand and encroach upon the lumen of the iter venosum (figs. 37F and 38F, *R.* and *L. C. D.* and *It. V.*). Next, the fore limbs develop, and send their venous blood by the subclavian veins into the ductus Cuvieri, and convert them into the superior venæ cavæ (fig 47G, *S. V.* and *V. C. S.*). This conversion is accompanied by a further encroachment of the veins upon the iter venosum, which persists for a time as a narrow chink between the vein and the alimentary canal, but this finally disappears (fig. 47G, *It. V.*). In the Rabbit the passage is largest at the end of the ninth and during the tenth day, and is closed by the commencement of the thirteenth. I have never seen its lumen divided in more than four or five of a series of longitudinal sections Its closure is assisted by the growth of the mesoblast round the trachea and œsophagus, and seems to be effected in the same manner in the Human embryo as in the Rabbit, as may be seen by comparing the accompanying drawing of a transverse section of an early Human embryo with those of the Rabbit (fig. 46, *It. V.*). In rare instances the iter venosum may persist, and I have seen in a Human fœtus an aperture at the inner side of the vena cava superior which opened from the pericardial into the pleural sac; this patency was associated with a tri-cœlian heart and other abnormalities

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* 'Entwicklungsgeschichte,' p 286.

† 'Entwicklungsgeschichte des Kaninchen-Eies,' pp 134 and 137, pl 15, figs 62 and 63

The closure of the passage which I have ventured to call the "iter venosum" is a matter of dispute. HIS, writing in 1881,[*] attributes the closure in Rabbits and Man mainly to the approximation of the Cuvierian ducts I myself had arrived at a similar conclusion before having seen HIS's paper. USKOW[†] mentions three main factors in the occlusion. 1. The general alteration in the position of the foremost part of the mesocardium laterale. 2. A thickening of the "massa longitudinalis" (a name which the author gives to the tissues along the side of the trachea and œsophagus). 3. A cell increase in the "massa transversa" (*i e.*, the dorsal part of the diaphragmatic mesoblast). This author also mentions the ducts of CUVIER in this connexion, but does not, in my opinion, attach sufficient importance to the part they play. The names "massa transversa" and "massa longitudinalis," which USKOW uses, seem to me superfluous.

Whilst the iter venosum is being occluded the lungs protrude from the œsophagus into the recessus abdominalis, and soon afterwards a septum, the dorsal pericardium,[‡] originates betwixt them and the heart. The development of the dorsal pericardium is preceded by changes in the cardiac endings of the great veins, due to a gradual expansion of the sinus reuniens, and therefore these changes may be mentioned before the septum. The sinus, as we have seen, is formed from the cardiac ends of the vitelline veins, and retains for a time the features of those vessels, and is situated at the dorsal edge of the primitive splanchnic retroflexion, or septum transversum. By the time the jugular veins have appeared the sinus reuniens has expanded and become more capacious, but it does not at first receive those vessels, for, as we have seen, they open into the ends of the umbilical veins (fig. 6, *A. C. V.*). As the expansion of the sinus reuniens proceeds it involves the mouths of the umbilical veins, and they are gradually merged into, and become part of, the sinus (fig. 36, *S. R.* and *L. U. V.*, also figs. 33E and 38F and 39F, *R. U. V.* and *S. R.*); and at last it progresses so far that the jugular veins (or ductus Cuvieri) acquire separate openings of their own (figs. 37F, 38F, *S. R.* and *R.*, and *L. C. D.*). Thus, by the time the lungs and pericardium have begun (eleventh day), the sinus reuniens receives on either side three great veins, namely, the vitelline, the umbilical, and ductus Cuvieri. At this stage it is situated at the dorsal part of the septum transversum, and not beneath it, as it is said to be in the Human embryo; moreover, it opens into the auricle by a wide mouth, and not by a narrow porta vestibuli;* also, by the time these changes have taken place in the terminations of the umbilical veins, each of those vessels has acquired communications with the hepatic venous spaces (fig. 41F, *R. U. V.* and *L. U. V.*), and, on the left side, this new communication ultimately becomes the ductus venosus Arantii.

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[*] "Mittheilungen zur Emb. der Säugethiere, &c.," 'Arch. für Anat. und Phys.,' 1881, p. 318.

[†] *Ibid.*, p. 174.

[‡] Called by some authors, SCHMIDT, HIS, and USKOW, *membrana pleuro-pericardiaca.*

The separation of the Cuvierian ducts from the umbilical veins is accompanied by an elongation of the mesocardium laterale, which becomes a short and thick septum, the dorsal pericardium, between the recessus *pulmonalis* and the pericardial sac. This septum begins in front at the ductus Cuvieri (figs 37F, 39F, and 40F, *D.P.*), and is continuous behind with the dorsal part of the septum transversum; which, after a while, also assists in the formation of the pericardium. At its junction with the septum transversum the dorsal pericardium widens out to transmit the umbilical veins (figs. 39F, 41F, and 42F, *R. U. V.* and *L. U. V.*). In subsequent stages, as the lungs grow and as the thorax develops, the dorsal pericardium increases in *width* (figs. 49G and 50G, *D. P.*), and as the lungs expand it gradually becomes an extensive and tenuous membrane, the permanent pericardium (fig. 57I, also fig. 62, *D. P.*). The *length* of the dorsal pericardium is at first insignificant, for it only reaches from the Cuvierian ducts as far as the septum transversum, or ventral diaphragm. Before the lungs develop the ducts and ventral diaphragm are close to one another (fig. 54H, *L. C D* and *V. D.*); but as those organs grow the thorax elongates and the ducts and diaphragm are carried apart, so that the pericardium becomes longer† (figs. 53 and 54H, *D. P.*); and this applies both to the Rabbit and to the Human embryo, and without doubt the mesoblast of the dorsal part of the ventral diaphragm, and in the neighbourhood of the sinus reuniens, assists by its elongation in its formation. Thus, the development of the pericardium is mainly dependent upon the expansion and elongation of the thoracic region which accompanies the development of the lungs But the formation of an air breathing apparatus entails changes in the heart and vascular septum which have also an influence. One of the events is the shrinking of the sinus reuniens and its ultimate conversion into the saccus reuniens (HIS).‡ This process is preceded by the obliteration of various portions of the umbilical and vitelline veins, and before its completion the pulmonary veins and left auricle have originated, and, moreover, the heart itself has travelled backwards away from the head. Both of the umbilical veins lose their cardiac openings as the thoraic portion of the embryo elongates; and as the liver develops the right vein disappears entirely, although traces of its trunk can be detected in the body wall for some time after it has ceased to perform any function. As the cardiac opening of the left umbilical vein closes, the communication which its trunk has previously acquired with the hepatic venous spaces (fig. 41F, *R. U. V.* and *L. U. V.*) gradually becomes more free, and at last (twelve and a half days), by dilatation of the spaces, a channel is formed in the liver substance, and, conveys the blood of the left umbilical vein across into the end of the right vitelline and so onwards into the sinus reuniens (figs 50G, 51G, and 52G). For some time after the obliteration of the cardiac end of the left umbilical vein its lumen persists in the body wall, in front of the commencement of the ductus venosus Arantii (fig. 52G, *L U. V.* and *D. V. A.*). After the closure of the cardiac ends of the umbilical veins the junction of the dorsal pericardium and septum transversum, through which they previously passed, remains as a solid septum betwixt the lungs and the heart.

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* HIS, 'Anat. Menschl. Embryonen,' pt 3, pp. 145 and 202

† HIS, *loc cit*, p. 146, attributes the formation of the dorsal pericardium to the separation of the Cuvierian ducts from the body wall.

‡ *Loc. cit.*, pt 3, p. 145.

After the development of the stomach and alimentary canal the course of the vitelline veins consists of three parts, a mesenteric, a hepatic, and a septal. The first and second of these hardly require an explanation, the third is a portion of each vitelline vein which lies between the liver and the sinus reuniens, and which projects dorsalwards from that chamber and the septum transversum into the recessus pulmonalis (figs 38F, 39F, *S.R. Vit. V.*) Inasmuch as both the vitelline veins do not share the same fate, they require to be considered separately. When the sinus reuniens has undergone expansion (11th day) the hepatic part of the left vitelline vein begins to be occluded with liver substance (fig. 42F, *L., Vit. V.*), and after a while the dorsal lobe of the liver no longer betrays any traces of its presence (fig. 51G, *D.L.*). Simultaneously the vein ceases to open into the sinus reuniens, although vestiges of it may be still found in the dorsal pericardium, close to where that structure is continuous with the septum transversum, or, as it may now be called, the ventral diaphragm (fig. 50G, *L., Vit. V.*). The mesenteric part of the left vitelline vein also disappears, except a short length near the vitelline duct, which makes its way into the right vitelline vein; this seems to be the only communication between the two vessels, and, although others have been described in Human embryos, the material in my possession leads me to think that some of them cannot be constant.*

The early obliteration of the septal and hepatic portions of the left vitelline vein has, without doubt, an adverse effect upon the development of the left lobe of the liver and also upon that of the left side of the pericardium and ventral diaphragm. Those structures, more particularly the left lobe of the liver and ventral diaphragm, develop less than the right, and in consequence the left recessus pulmonalis is the most capacious. Under these circumstances, it may be assumed that it would require a greater developmental effort to partition the left recessus pulmonalis from the peritoneum than the right, and, therefore, that failures would be commonest on that side. This is actually the case, for we find that, although congenital absence of the hinder part of the diaphragm is common on either side, yet it is commonest on the left in the proportion of five to one.[*]

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* His, *loc. cit.*, p. 202.

As far as we have followed the history of the right vitelline vein, it has passed through the following stages :—At first it carried blood back from the vascular area; then this was augmented with that from the umbilical veins and liver, and afterwards with the whole of the blood of the left umbilical vein through the ductus venosus Arantii. Before the ductus venosus develops the septal part of the right vitelline vein lies close to the body wall upon the dorsum of the sinus reuniens and septum transversum (figs. 38F and 39F, *S.R.* and *S R. Vit. V.*). But after the obliteration of the cardiac ends of the umbilical veins, the shrinking of the sinus reuniens, and the formation of the dorsal pericardium, it is separated from the body wall, and instead of projecting into the recessus pulmonalis lies more in the substance of the dorsal pericardium (fig. 50G, *R. Vit. V.*). It is still close to the sinus reuniens, but that chamber has become smaller and has to a large extent disassociated itself from the septum transversum, and lies between it and the heart (fig. 55H, *S R.*, also fig. 57I, *S.R.*). As the thorax and pericardium develop the likeness of the septal portion of the right vitelline vein to the thoracic part of the vena cava inferior becomes unmistakable (figs. 60I and 61I, *V.C.I*).[†] And, in addition, whilst the change is being effected, the hinder part of the vena cava inferior develops and sends its blood to the heart by the vessel in question. The vena cava inferior appears both in Rabbits and in Human embryos either before or simultaneously with the permanent kidneys (beginning of 13th day in the Rabbit). It commences a little in front of those organs by two blind symmetrical rootlets (the renal veins), situated at the base of the mesentery, and in front of the aorta. After communicating with both posterior cardinal veins, especially with the right, it runs forwards by the side of the aorta, and enters the liver and runs through the substance of that organ to empty into the right vitelline vein in front of its junction with the ductus venosus Arantii. The vena cava enters the liver through a junction (the caval junction) which that organ previously acquires with the tissues at the base of the mesentery (fig. 52G, *C.J.*). The right vitelline vein also receives numerous branches from the stomach, pancreas, spleen, and intestines as those organs develop, and becomes the portal vein (fig. 54H, *R. Vit. V.*). It retains for a time its direct communication with the ductus venosus, but finally its lumen becomes occluded with liver substance, and it ends in small channels, which are the beginning of the interlobular veins.[‡]

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[*] Lichtenstern, 'Cyclopædia of the Practice of Medicine,' Ziemssen, vol. 7, p. 554

[†] His calls this part of the right vitelline vein the ductus venosus Arantii, *loc cit*, p. 102, fig 100.

[‡] So many different accounts are given of the development of the venous system that it would be a very lengthy task to collate them Kölliker, in his 'Entwicklungsgeschichte,' p 915, gives a clear account of them. That which I have given accords most nearly with His's description (*loc. cit.*, p 207), with the exception of the thoracic portion of the vena cava inferior and of the various communications between the vitelline veins

In the higher Mammals the diaphragm usually consists of three parts—namely, of a central part, in relation with the pericardium and heart; of lateral parts, which are muscular; and of crura. So far I have only traced the origin of the central part, that which is interposed between the heart and liver. This is at first a thin layer of mesoblast, whose cells are arranged transversely (figs. 42F and 43F, also figs. 53 and 54H, *S. T.* or *V. D*). In many animals, *e.g.*, the Dog, Rabbit, and Man, it splits towards the end of intra-uterine life into two distinct layers—a superior, which helps to form the pericardium; and an inferior, which usually becomes tendinous, and is the tendinous centre of Human anatomists. In Man the fibrous pericardium and tendinous centre reunite after the third year, but they remain permanently apart in many Mammals, the azygos lobe being interposed between them. During the time that the Human pericardium is separable from the diaphragm it invests the thoracic part of the vena cava inferior with both its fibrous and serous layers, and these investments never entirely disappear. Further, although the liver also disassociates itself very widely from the central part of the diaphragm (figs. 63J and 64J), yet it always retains part of its original connexions by means of the lateral, coronary, and falciform ligaments. These are so arranged in most of the higher Mammals that they bisect each leaflet of the tendinous centre, and do not as a rule pass beyond their limits. The coronary ligament is complicated by the caval junction and by the development of the remaining portion of the diaphragm, the dorsal diaphragm, which will be described presently.

The sides of the diaphragm begin to develop at the same time as the lungs, and increase as the thoracic region expands. They begin as a constriction between the liver and the body wall (fig. 43F, *L.D.*), and this constricted part gradually becomes longer (figs. 51G and 60I, *L.D.*), and is finally converted, in a greater or less degree, into muscular tissue.

When the iter venosum of the Rabbit or of the Human embryo is just on the point of closure, a mesoblastic process, the dorsal diaphragm (USKOW), grows from the body wall across the recessus pulmonalis, and ultimately partitions it from the hinder part of the pleuro-peritoneal cavity and thus completes the diaphragm. The ingrowth is the same on either side, and originates far forwards, close to the Cuvierian ducts. When it is first discernible the lungs are simple diverticula from the sides of the œsophagus (figs. 49G and 55H, *Lng.*). During its early stages the dorsal diaphragm has hardly any of the characters it ultimately attains, and, therefore, it is desirable to consider it at a stage at which its identity is not doubtful, and, yet, at which it has not lost its earlier peculiarities.

The accompanying figure was made from a coronal section through a Rabbit's embryo of the early part of the fourteenth day (fig. 35, *D.D.*). It would have been better, perhaps, had the specimen been a little less advanced; but, nevertheless, it suffices to exemplify the point I wish to make clear, namely, that the lateral attachments of the dorsal diaphragm to the side body wall are nearer the head than its median connexions. At this period, the fourteenth day, the various organs are well grown, and it is easy to recognise the dorsal diaphragm between the lungs and liver. It is a V-shaped structure, arranged so that the apex of the V blends behind with the dorsal mesentery, whilst its arms spread forwards and outwards to unite with the body wall. It is easy to infer, and presently it will be seen, what such a diaphragm would look like in transverse sections, but it is clear that, the series being begun in front, the attachment to the body wall would come into view first, and afterwards the more median portions. The dorsal diaphragm is at first (twelve and a half days in the Rabbit) of small extent, and it may only be found in seven sections of a series. Judging from both longitudinal and transverse sections, it is a partial crescent-shaped septum which grows from the body wall just behind the Cuvierian ducts (fig 55H, *D.D.*, also fig. 48G), but is incomplete posteriorly, where its free crescentic margin projects into the pleuro-peritoneal cavity. Its dorsal attachment is just in front of the foremost end of the uro-genital ridge; ventralwards it blends with the dorsal pericardium (figs. 49G and 50G, *D.D.*), and grows tailwards along it, until, at last, it fuses with the dorsal lobe of the liver and, on the right side, with the wall of the vitelline vein, or, as it may be called, the vena cava inferior (fig. 50G, *D.D.* and *R. Vit. V.*). On the left side the vitelline vein has almost disappeared, but its remains may sometimes be seen in the pericardium, opposite the attachment of the dorsal diaphragm (fig. 50G, *L. Vit. V.*). As sections approach the hinder part of the dorsal diaphragm the whole of its extent is not divided, but only its dorsal and ventral ends It seems unnecessary, as USKOW has done, to give names to these parts, for they have, in my opinion, no special significance. their presence is explicable if it is true that the shape of the hinder edge of the dorsal diaphragm is crescentic. In addition to the foregoing the dorsal diaphragm has two surfaces, of which one, the pleural, faces and is almost in contact with the lungs, which, before its completion, project beyond it into the hinder part of the pleuro-peritoneal sac; and another surface, the peritoneal, which is separated from the side body wall by a portion of the peritoneal cavity.

It seems hard to tell why the dorsal diaphragm should originate so far forwards. Before the vitelline veins and ductus Cuvieri separate there is, however, a process of mesoblast in the angle between them which would tend to become larger as the veins went apart (fig. 45, *D.D.*). This process is in the position of the dorsal diaphragm, and may not improbably form its starting point.

The dorsal diaphragm is incomplete and close to the foremost end of the pleuro-peritoneal sac when the cartilaginous vertebral column and ribs develop. At that time (beginning of thirteenth day in the Rabbit) the lungs, although larger, are still mere diverticula; but the pulmonary veins have originated as channels in the mesoblast which is common to them and to the œsophagus, and empty themselves into the left auricle (fig. 57I and fig. 62, *P. V.*). The dorsal diaphragm has also travelled tailwards away from the superior venæ cavæ, and is, in front, united solely to the body wall (fig. 56, *D.D.R.* and *D.D.L.*). As it runs inwards towards the mesentery it unites with both the uro-genital ridge and with the pericardium (figs. 59I and 60I), and, finally, with a triangular mass of mesoblast which covers the dorsal lobe of the liver (figs. 59I and 60I). As yet its hinder edge is crescentic, and the lungs project beyond it into the peritoneum; but this protrusion gradually becomes less apparent (fig 64J, *Lng.* and *D.D.*). A gradual separation of the dorsal diaphragm and mesonephros from the superior venæ cavæ accompanies the growth of the thorax. By the time the dorsal diaphragm is on the point of uniting with the mesentery it has both grown and been carried tailwards so far that its median part unites with the mesoblast which covers the dorsum of the liver some distance beyond its junction with the pericardium (fig. 63J, *D.D.*). And, in consequence, the hepatic mesoblast takes a share, as CADIAT claims, in forming the diaphragm.*

The final closure of the aperture between the dorsal diaphragm and the mesentery has no particular feature. Before it is accomplished muscular fibres are abundant in the position of the crura and wherever the diaphragm springs from the body wall. All of these originate *in situ*, and those of the crura begin the earliest (12½ days) in the base of the mesentery (fig. 54H, *Cr. D*). After a while (14th day) they become quite distinct, and consist of bands of muscular fibres situated in front of the cartilaginous bodies of the vertebræ and at the base of the mesentery. These fibres run ventralwards round the sides of the œsophagus to spread out in the dorsal part of the ventral diaphragm, and some of them almost surround the vena cava inferior.

After the diaphragm has become a complete septum the history of its development would mainly relate to the gradual growth of the structures whose origin has been described and their gradual approximation to their permanent condition. These processes are unaccompanied by any remarkable circumstances. The main factor associated with them is the expansion of the lungs, which, in the higher types, spread ventralwards round the sides of the pericardium (fig. 62) and forwards between the superior venæ cavæ and the body wall; but, as none of these ever affect the principles of the processes which I have endeavoured to explain, I do not propose, at present, to pursue them further. However, the recess, apical recess, between the Cuvierian ducts, or superior venæ cavæ, and the body wall seems to commence at an early stage of development (figs. 37F and 39F, *R*).

Finally, I may add that the following conclusions have been arrived at:—

1. The heart develops from splanchnopleure into the foremost end of the cœlom, which afterwards becomes the pericardial sac.

2. The cardiac portion of the cœlom is cut off by (*a*) the vitelline veins; (*b*) the Cuvierian ducts.

3. The mesocardium laterale is a point at which the mesoblast is uncleft, and at which on each side the somatic umbilical vein is transmitted into the splanchnic vitelline vein. Afterwards the mesocardium laterale transmits the Cuvierian ducts.

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* "Du Développement de la Portion Céphalo-thoracique de l'Embryon, &c.," 'Journal de l'Anatomie,' vol. 14, 1878, p. 620.

4. The umbilical veins commence in a portion of body wall which, after the rotation of the embryo, becomes the fœtal placenta. (This applies to Rabbits, and probably to Human embryos.)

5. The precedence of the great veins is as follows:—1, vitelline; 2, umbilical; 3, anterior cardinal, 4, posterior cardinal, converting a portion of anterior cardinals into the Cuvierian ducts. The whole of the right umbilical, the cardiac end of the left umbilical, and the left vitelline vein disappear, and the right vitelline becomes the portal and cardiac end of vena cava inferior. (This only applies to the early changes, and, perhaps, a small length of the commencement of the left vitelline vein may also persist.)

6. The dorsal pericardium originates from the mesocardium laterale and dorsal part of the septum transversum, the rest of the latter becoming the ventral diaphragm, *i.e.*, that between the liver and the heart.

7. The dorsal diaphragm is an ingrowth from the body wall into the recessus pulmonalis.

ABBREVIATIONS.

A. B.	Aortic bulb.
D. A.	Dorsal aorta.
Ao.	Aorta.
All.	Allantois.
All. V.	Allantoic vein.
All. Art.	Allantoic artery.
Al. C.	Alimentary canal.
Am.	Amnion.
Aud. Ep.	Auditory epithelium.
Au.	Auricle. R. right; L. left.
Az. V.	Azygos vein.
Blas.	Blastoderm.
B. A.	Aortic bulb.
Br. A.	Branchial arch.
Br. C.	Branchial cleft.
B. W.	Body wall.
Blas.	Blastoderm; *P. B.*, peripheral blastoderm.
C.	Cœlom.
C. C.	Cardiac cœlom.
C. V. Ant. and *P.*	Cardinal veins—anterior and posterior.
C. D.	Cuvierian ducts.
C. J.	Caval junction.
C. S.	Cardiac end of stomach.
Cr. D.	Crus of diaphragm.
D. A.	Dorsal aorta.
D. D. R. and *L.*	Dorsal diaphragm—right and left.
D. P.	Dorsal pericardium.
D. L.	Dorsal lobe of liver.
D. S. T.	Diaphragmatic portion of septum transversum.
D. V. A.	Ductus venosus Arantii.
End. Ht.	Endothelial lining of the heart.
Ep.	Epiblast.
F. B.	Fore-brain.
F. L.	Fore-limb
G.	Gut.
H. L.	Hind-limb.
Hd.	Head.
H. G.	Hind gut.
Ht.	Heart.
Hy. A.	Hypogastric artery.
Hy.	Hypoblast.
H. Hy.	Hepatic hypoblast.

I. F	Interamniotic foramen.
It V.	Iter venosum.
J. V.	Jugular vein.
L.	Liver.
Lng.	Lung.
L. D.	Lateral portions of diaphragm.
M.	Mouth.
M. A.	Mandibular arch.
M. B.	Mid brain.
M. L.	Mesocardium laterale.
Mes. Ant. and *Post.*	Mesocardium—posterius and laterale.
Mes. D. and *V.*	Mesentery—dorsal and ventral.
M. V.	Mesenteric veins.
Œs.	Œsophagus.
P.	Peritoneal sac.
P. Am.	Pro-amnion.
P. C.	Pericardial cavity.
P. Div.	Pulmonary diverticulum.
P. M.	Peripheral uncleft mesoblast.
P. N.	Pronephros.
P. P. C.	Pleuro-peritoneal cœlom.
Plac.	Placenta.
Pl.	Pleural cavity.
P. V.	Pulmonary veins.
R.	Apical recess.
R. Ab.	Recessus abdominalis.
R. Pul.	Recessus pulmonalis.
S. M.	Spinal medulla.
So	Somatopleure.
S.	Spleen.
Spl.	Splanchnopleure.
Spl'.	Hinder part of splanchnopleure.
St.	Stomach.
S T.	Septum transversum.
S. R.	Sinus reuniens.
S. R. Vit. V.	Septal portion of right vitelline vein.
S. V.	Subclavian veins.
T.	Tail.
Th. D.	Thoracic duct.
Tr.	Trachea.
Ut.	Uterus.
U. V.	Umbilical vein.
Ven.	Ventricle.
V. D.	Ventral diaphragm.
V. Ht.	Venous end of heart.
Vit. V. R. and *L.*	Vitelline vein—right and left.
Vit. D.	Vitelline duct.
Vil. P.	Villous projections.
V. C. S.	Vena cava superior.
V. C. I.	Vena cava inferior.
W. B.	Wolffian body.
W. D.	Wolffian duct.
W. T.	Wolffian tubule.

DESCRIPTION OF FIGURES.

The addition of a letter to any number implies that those drawings were made from the same embryo or series of sections.

Fig. 1. Rabbit. Commencement of eighth day.
Fig. 2. Rabbit. Middle of eighth day.
Fig. 3. Rabbit. Second half of eighth day.
Fig. 4. Rabbit. Beginning of ninth day, ventral aspect.

Fig. 5. Rabbit. Nine days and four hours. Longitudinal section through the iter venosum.

Fig. 6. Rabbit. Nine days and a half Sinus reuniens receives umbilical vein, and latter receives the jugular or anterior cardinal vein.

Figs. 7A to 14A. Longitudinal sections of Rabbit's embryo at beginning of ninth day. This series demonstrates the continuity of the cardiac and pleuro-peritoneal cœlom behind the vitelline veins, and also the opening of the umbilical vein into the vitelline.

Figs. 15B to 19B. Transverse sections of Rabbit's embryo of nine days and four hours. This embryo closely resembled fig 4. The series consisted of 153 sections. 15B = sec 19. 16B = sec. 44. 17B = sec. 57. 18B = sec. 77. 19B = sec. 139.

Figs 20C to 22C Coronal sections of Rabbit's embryo of nine days and five hours·—

20C. Through iter venosum.
21C. Through sinus reuniens.
22C. Through septum transversum and liver.

Figs. 23D to 30D. Rabbit's embryo of second half of ninth day. Liver, placenta, course of veins, and relation of embryo to wall of uterus (after it has undergone rotation).

Fig. 30. Placental region of Rabbit beginning of tenth day.

Fig. 31. Coronal section through Rabbit's embryo at beginning of tenth day. The relation of embryo to wall of uterus and placental region, especially the relation of placental region to hinder part of the splanchnopleure.

Figs. 32E to 34E. Longitudinal sections of Rabbit's embryos of nine days and sixteen hours.

32E. Through iter venosum.
33E. Through Cuvierian duct, jugular and posterior cardinal veins, umbilical vein, and sinus reuniens. An arrow has been placed in the iter venosum
34E. Relation of umbilical vein to duct of CUVIER (through outer wall of iter venosum).

Fig. 35. Coronal section of Rabbit's embryo of fourteen days, to show the dorsal diaphragm.

Fig. 36. Almost transverse section through Rabbit's embryo of nine days and sixteen hours at level of Cuvierian duct and iter venosum. The villous projections of the liver and venter are shown.

Figs. 37F to 44F. Transverse sections of Rabbit's embryo of latter part of tenth day, to show sinus reuniens and septum transversum, liver, and great veins.

Fig. 45. Coronal section of embryo of latter part of tenth or eleventh day, to show great veins and commencement of dorsal diaphragm.

Fig. 46. Early Human embryo. Transverse section through Cuvierian duct and venosum.

Figs. 47G to 52G. Transverse section through Rabbit's embryo of twelve and a half days, to show the closure of the iter venosum and the development of the dorsal diaphragm.

Fig. 53. Human embryo 21 days (?). Showing the dorsal pericardium and ventral diaphragm.

Figs. 54H and 55H. Longitudinal section of Rabbit's embryo of twelve and a half days.
54H. Great veins, dorsal pericardium, and ventral diaphragm.
55H. Commencement of dorsal diaphragm.

Fig. 56. Transverse section of Human embryo. Dorsal diaphragm and dorsal pericardium.

Figs. 57I to 61I. Rabbit's embryo of thirteen days. Pulmonary veins, diaphragm, and pericardium.

Fig. 62. Rabbit's embryo. Pulmonary veins and pericardium.

Figs. 63J and 64J. Human embryo. Relation of dorsal diaphragm to the liver and ventral diaphragm.

XIV *On the Structure and Development of the Wing in the Common Fowl.*

By WILLIAM KITCHEN PARKER, *F.R.S.*

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[PLATES 62–65.]

INTRODUCTION.

OF late years, while the structure of the skull has greatly occupied me, the rest of the skeleton has been neglected in comparison A quarter of a century ago, or more, the whole skeleton, in Birds especially, occupied much of my thought; and from an even earlier period I have never ceased to gather together embryos and young Birds of all kinds, which should some day serve for a renewal of the work

In this short paper, dealing with a single region, and that principally in a single type, I give the first-fruits of a revised study of the Bird's skeleton. Many recent workers have dealt with the development of one part or other of the Bird's wing, but it seemed to me that we had from none of them a minute account of the successive changes in any one form. And now, having made such a study, I think I have not failed to draw some new facts from it.

I have carefully worked out the structure of the carpus in the Chick of seven days and older. I find that the two persistent carpals of the Bird's wing, the *radiale* and *ulnare* of authors, show evidence of being compound structures, probably containing within themselves remnants of an *intermedium* and a *centrale* The distal row of carpal elements was particularly in want of further study. I have figured various stages in the development of the three elements which constitute it, and have traced them up to their final vestigial rudiments in the co-ossified "carpo-metacarpus" of the adult. All these points I have verified by an examination of many other, principally Gallinaceous, Birds.

Next, I have traced the development of the three metacarpal bones, with their changes in form and in position. In connection with them I find certain small cartilaginous elements, which soon lose their independence, but leave traces in the full-grown wing, viz. (*a*) a cartilage to the radial side of the first metacarpal, in the position occupied by the spur of many Birds, which calls to mind the *pre-pollex* described by

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* Under the title "The Morphology of Birds" (see 'Proceedings,' vol 42, p 52).

BARDELEBEN, KEHRER, and others, in Amphibians, Reptiles, and even Mammals, (*b*) a cartilage to the ulnar side of the third digit, which probably is a remnant of the aborted fourth digit; and (*c*) certain cartilages of more doubtful nature developed in connection with the index finger, to its ulnar side, and afterwards fusing with it.

Lastly, I have made new observations on the small distal phalanges in the Fowl and other Birds, and on the rudimentary nails or claws of the second and third digits, and I have added a short revision of the structure of the wing through the Ratitæ.

Since GEGENBAUR* spoke the last weighty word upon the structure of the Bird's wing, no new facts have transpired to make us re-open the question of the homologies of the three digits with the pollex, index, and medius of other groups. Nothing in the skeleton, the muscles, or the development of the limb contradicts this acceptation, to the best of my knowledge. I take it for granted accordingly in this paper †

The Development of the Carpus

In the seven-days Chick, the hyaline cartilages of the wrist are still somewhat indefinite in outline, and imperfectly solid.

The elements which form subsequently the two permanent carpals are clearly visible (Plate 62, fig. 1, *c.u.*, and *i r*), and are developed in close relation with the extremities of the radius and ulna. The one to the radial side is very much the largest, as well as the most solid, of the carpal elements at this stage. Its distal end gives support to the pollex, and proximally it passes upwards in a great wedge between the radius and ulna. In the Fowl this element is from the first single, yet its shape and position at this period suggest that it contains in itself the equivalent of an *intermedium* as well as of a *radiale.* In certain Birds, *e.g.*, the Falcons, I have found that it actually divides afterwards into two sub-equal masses, and in one Bird at least, the Yellow Warbler (*Dendrœca æstiva*), the intermedium carpi has been already figured‡ in such a position as to indicate its severance from the *radiale.* I look, then, upon the so-called *radiale* of the Fowl's wing as really a compound structure, and shall designate it as *intermedio-radiale* for the future.§

The element on the ulnar side, the *ulnare* of the adult, is a much smaller, sub-crescentic mass of cartilage, lying to the free side of the pointed extremity of the ulna, but wedging its way, towards the middle line of the carpus, into contact with the *intermedio-radiale.* The "ulnare" is known to have in many Birds a remarkable extension towards the centre of the carpus, and in some cases it has been found to be actually double. Long ago I found in one of the Palamedeæ, viz., *Chauna chavaria,*

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* 'Carpus u. Tarsus,' 1864.

† This view is however dissented from by OWEN, WYMAN, and COUES.

‡ MORSE, 'Annals Lyceum Nat Hist., New York,' 1874, p. 146, fig 44.

§ Both in this Bird and in the seven-days Chick we notice especially how the intermedial element is wedged far up between radius and ulna, as GEGENBAUR found it in *Menopoma*, *Emys*, and some others, but more abundantly in the hind limb.

two ulnar carpals, apparently an *ulnare* proper and a *centrale.* More recently, in a more normal Chenomorph, the Falkland Island Goose (*Chloephaga poliocephala*), I found the ulnare nearly divided into two segments. And MORSE (*loc cit*) has already figured in the King-bird (*Tyrannus*) an independent nucleus, supposed to be the *centrale*, in close relation with the *ulnare* on its outer or radial side. I am inclined, therefore, to think that this ulnar carpal in the Fowl represents, like its radial fellow, two elements; and I propose to call it the *centralo ulnare.**

The result at which we have arrived in regard to the fusion of *intermedium* and *centrale* with *radiale* and *ulnare* respectively is a somewhat surprising one A study of the carpus in Amphibia and Reptilia seldom, if ever, shows an arrangement of parts which would lead naturally to such a coalescence. On the contrary, the ulnare and intermedium, the radiale and centrale are the parts that come into close relation. Ulnare and intermedium fuse together, for instance, in *Salamandra*, *Triton*, and probably in many Lizards; radiale and centrale in *Emys* On this account GEGENBAUR (*loc. cit.*) dismissed the supposition that the large *radiale* of the Crocodile, which juts up between radius and ulna, had included the intermedium with itself. But the position and relations of this element are, perhaps, worth re-examining, though BAUR† declares that no trace of intermedium (*i.e.*, no distinct centre of ossification or separate cartilage) exists in the Crocodilia at any time.‡ In the Mammalia such a fusion of intermedium and radiale ("scapho-lunar") is, of course, a common thing.

In the distal region of the carpus the Fowl shows at no period more than three separate elements. In this earliest (7-day) stage, two only are recognisable (Plate 62, fig. 1, *d c*^{2}, *d.c.*^{3}). The larger of these two lies in the middle of the carpus, and is in contact both with the intermedio-radiale and the centralo-ulnare. Its distal surface forms a concavity to receive the base of the second digit. An evident crowding of cells in the embryonic cartilage towards its radial side is the beginning of the formation of the first *carpale* (*d c.*^{1}), which will be seen distinctly in the next stage The third carpale (*d.c.*^{3}) is already distinct, lying in close relation with the base of the third digit.§

In the next stage, on the 8th day of incubation (Plate 62, fig. 2), the various carpal elements are all more solid and definite in form. The *centralo-ulnare* is becoming bilobate, and has increased considerably in relative size, so as to be little less than the

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* ROSENBERG ('Zeitschr Wiss Zool,' vol 23, 1873) comes to a different conclusion; he finds in the Chick a *radiale* and an *intermedio-ulnare*, but his statements regarding the distal part of the carpus are very different from mine. His paper contains a copious bibliography, and a summary of previous authors' views.

† 'Zool. Anzeiger,' 1885, No 208.

‡ In *Chamæleon*, STECKER states that an intermedium is present at an early stage, but disappears without coalescing with any other element. 'Sitzber. k Akad. Wiss,' Vienna, 1877, Abth 1, *cf* Dr. GUSTAV BORN, "Carpus und Tarsus der Sauria," 'Morphol Jahrb,' vol. 2, 1876, pp. 1–27, pl. 1.

§ The distal row of carpalia in Birds was detected by BORN (*l c*).

intermedio-radiale. The three distal carpalia are now all distinct, the middle one being still the largest, the inner the least. They form an arched row with a concavity towards the manus, so that the middle metacarpal (*mc.*^{2}) is wedged in between the first metacarpal and the third distal carpal.

Already at the end of the tenth day (Plate 62, figs 3, 4) important changes have taken place, involving some *displacement of parts* in the carpus. The small first distal carpale (*d.c.*^{1}) has been arrested in its growth, and is now only one-tenth as large as the second; and it has been, so to speak, thrust out of its place by the great second metacarpal, on the flexor or inner side of which it is developed The third distal carpale, also comparatively small, being about one-third the size of the second, belongs to the ulnar side of the wrist, where it lies, a slender rod of cartilage, at the base of the third digit, looking at this stage from its elongated form more like a metacarpal than a carpal element Its slender distal end soon unites with the proximal end of the third metacarpal.

We may now pass over two or three stages in which other parts of the limb undergo important development, while the carpus remains little changed. At hatching the carpus is still devoid of any centres of ossification, and my first figure which shows these is that of the Chick thirty-three days old (Plate 62, fig. 10). Here we see that the *centralo-ulnare* contains a large bony centre, while the *intermedio-radiale* is still purely cartilaginous. The third distal carpale shows a small bony nucleus. The small first distal carpale, somewhat increased in size, has acquired a pyriform outline, its smaller end being turned towards the pollex.

In ten or twelve days more, that is to say in the Chick of six weeks old (Plate 62, fig. 11), the intermedio-radiale has acquired a small round bony centre near its outer or radial edge, and the second or median distal carpale has a large oval core of bone. The third distal carpale is conspicuous, with a long oval bony centre.

In a Chicken three-quarters of a year old (Plate 62, fig. 12, and Plate 63, fig. 1) the wing is still far from perfect, as I have elsewhere shown to be the case of the skull also. While the Chick at hatching-time is as ripe as a Pigeon a fortnight after hatching (though proportionately much less in size), after eight or nine months of growth it is still as undeveloped as a Pigeon a month or five weeks old. The two large permanent carpal bones, those, that is to say, of the proximal row, now alone remain distinct. The second and third distal carpals have united with one another and with the metacarpus, but may still be distinctly seen from both flexor and extensor surfaces. The displaced first carpale is now ossified, and shows conspicuously as an oblong lobe of bone, placed transversely across the flexor surface of the base of the middle metacarpal.

In the full-grown Hen (Plate 63, figs. 2, 3) all the original outlines of the distal carpals have become obliterated.

A number of other Gallinaceous Birds, to which I shall refer in treating of the carpus, show no important discrepancies in the structure of the carpus. They vary somewhat in the relative sizes of the carpal elements, and the period at which these ossify. In the Argus Pheasant, for instance (Plate 63, figs 9, 10), the intermedio-radiale, which ossified late in the Fowl, contains its ossifying centre at the time of hatching, before any of the other carpal elements In the newly hatched Partridge, both intermedio-radiale and centralo-ulnare are ossifying, in the Quail, neither; and so on. The figures show these and other points sufficiently well. But with all this variability in detail, the essential features are constant in all the forms examined; and so, though we get no great help from these Gallinaceous Birds in elucidating the compound nature of the proximal carpals, the number, position, and ultimate fate of the three distal carpals are made clear.

The Carpus in the Ratitæ.

The following is a brief review of the composition of the carpus in Ratite Birds.

In *Dromæus ater* (Plate 65, fig. 4) I can find no trace of carpal elements either in the young or adult bird.

In *Apteryx Owenii* (Plate 65, fig. 5) and *A. australis* I find no visible carpals in the adult[*]; the three fused metacarpals unite by a synchondrosis with the radius and ulna.

In *Casuarius galeatus* (adult, Plate 65, fig 6) I find a small triangular *ulnare* wedged in upon the ulnar side of the wrist-joint. No other carpal element is perceptible [†]

In *Struthio* (Plate 64, fig. 12) we have a much more normal wing. A very instructive preparation of the wing of a young Ostrich exists in the Hunterian Museum. Here we see the *radiale* and *ulnare* distinct and separate, and the latter already ossified Wedged in between and below them is a mass of bone as large as both together, which represents the distal carpals. Probably it originated in the embryo in three segments, but we have no evidence here of any such displacement of the first of these as we have studied in the Carinate bird.[‡]

The wing of *Rhea* has been figured in a young specimen by Dr R. O CUNNINGHAM.[§] The large distal carpal mass seems to show signs of having been in three parts, and is independent of the metacarpals In the adult (Plate 65, fig. 1) there is to be seen on the flexor surface of the proximal end of the second metacarpal, a nodule of bone, which, from the analogy of the typical Carinate wing, may I think be the displaced

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[*] WIEDERSHEIM ('Lehrbuch,' p 186) speaks of a *radiale* both in *Apteryx* and *Casuarius* OWEN also speaks of a carpal ossicle in *Apteryx*. I cannot find it in the adult I hope that this and other points will soon be settled in the embryo of *Apteryx* by my son, Prof T J PARKER

[†] MECKEL found the carpus of a Cassowary containing one ossicle (*ulnare*) in one wing, and two in the other (MECKEL's 'Archiv,' vol. 13, p 229, 1830) STANNIUS found one invariably ('Lehrbuch,' p. 259.)

[‡] ALIX describes minutely the somewhat peculiar shape of the *ulnare* in the Ostrich ("Sur l'appareil locomoteur de l'Autruche," 'Bull. de la Soc. Philom,' 1867, also 'App. locomoteur des Oiseaux,' Paris, 1874, p. 321).

[§] 'Zool. Soc. Proc.,' 1871, pl. 6A

first *carpale.* The other two distal carpalia are quite obsolete. The *radiale* and *ulnare* are free bones, but unlike their counterparts in the Carinatæ in shape. The *ulnare* is here a simple transversely elongated bone; the *radiale* is much larger, and constricted half-way across by a deep fissure or cleft. This anomaly demands further study of the embryo for its elucidation; it is not unlikely, to my thinking, that the two portions of the forked "*radiale*" will be found to answer, the smaller to the *radiale* proper, the larger and inner segment to the *intermedium.*

The Metacarpus.

Anatomists since CUVIER have generally recognised the Avian metacarpus as consisting of three coalesced elements, the metacarpals, namely, of the pollex,* index, and medius, which are all very distinctly (if rather diagrammatically) figured in the Chick by GEGENBAUR ('Carpus u. Tarsus,' Plate 3, fig. 3).

The following is an account of the growth and ossification of these elements in the Chick:—

In the Chick of the 7th day (Plate 62, fig. 1) the three metacarpals are completely separate. That of the pollex is about one-third the length of the next in order, and is unossified. The second is the largest; its middle third is ossifying; and in the same region the little rod-like bone is bowed inwards and away from the third digit to form the lanceolate space for the interosseous muscles. The third metacarpal is a little shorter than the second, and only two-thirds as thick: it also is ossifying in its middle third.

By the eighth day (Plate 62, fig. 2) the two larger metacarpals are getting a well-defined ectosteal sheath, but the pollex is still wholly cartilaginous. The metacarpal of the pollex is still opposite to its own carpale, but the other two metacarpals are as it were wedged into the carpal region, and have displaced the outer carpale.

A reference to the figures on Plate 62 will make plain the progress of ossification and the change in the relative size of these metacarpal elements. It will be seen that at the time of hatching (fig. 9) the metacarpal of the pollex is quite destitute of an osseous centre, and that, at that period, it seems to form part of the general mass of cartilage in which the distal carpals and the proximal extremities of the metacarpals have for the most part lost their independence.

In the Chick of a month old (fig. 10) the first metacarpal is well-ossified, and coalescing with its larger neighbours.

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* CUVIER, 'Leçons,' 1st edit, vol 1, p 314. 'L'os du métacarpe porte, au côté radial de sa base, sur une apophyse particulière, *ou même un petit os séparé*, un os stiloïde qui tient lieu de pouce.' See also 2nd edit., vol. 1, p. 438. The *metacarpale pollicis* is treated by TIEDEMANN, WIEDEMANN, and even STANNIUS ('Wirbelth.,' p. 259) as an apophysis merely. HEUSINGER (MECKEL's 'Archiv,' vol. 6, p. 548, 1820) calls attention to its distinctness in Raptores, and especially in Owls; he mentions having seen it almost completely separate in one- and two-day-old Pigeons, and completely separate in an Owl of about the same age.

In connection with these three well-known and generally recognised metacarpals there exist at least three inconspicuous vestiges, which I have carefully studied in the hope of finding in them evidence of missing digits. More than one author has sought, and fancied that he had found, traces of additional metacarpal elements , and I have tried to trace the development of the several structures which have seemed to others to be of this nature.

In very many Birds (most Gallinacei, many Passerines, &c.) the interosseous space between the metacarpals of the index and third finger is partially crossed by a bony process jutting out from the former bone (Plate 63, fig 1, *mc.*$^{2'}$). It is connected with the insertion of the *extensor carpi ulnaris* (SELENKA ; *flexor metacarpi radialis*, TIEDEMANN, HEUSINGER, &c.) This structure HEUSINGER[*] long ago looked upon as a rudimentary metacarpal of an aborted middle finger. He describes it as present in a more or less obvious state in almost all Birds, and he found it a distinct and separate ossicle on one occasion in a six-months-old Hen. The flattened proximal phalanx of the index, which sometimes juts forwards into a free point on its ulnar side, and is sometimes partially divided by a longitudinal groove or even by unossified vacuities,[†] contains, according to him, the coalesced rudiment of a phalanx of the same missing digit.

This so-called metacarpal rudiment is not to be found in the earliest Chick that I have examined, but it appears on the tenth day as a lanceolate patch of true cartilage on the ulnar side of the second metacarpal, about its own length from the proximal end of the large rod, and one-fifth of the length of the latter Its inner side is flattened against the main rod, while its outer edge projects over the next or third metacarpal (see Plate 62, fig. 3, *mc.*$^{2'}$) Already by the twelfth day this structure is arrested in its development, and forms now a simple oval patch lying well between the two larger metacarpals. By the fourteenth or fifteenth day (Plate 62, figs. 7, 8) it appears smaller ; in my preparation of the Chick six weeks old it is still a distinct piece of hyaline cartilage that seems to have kept pace in its growth with its larger neighbour ; but it is much reduced in the young Fowl of nine months. My preparations do not show a separate centre of ossification for this process, but it must have one, at least occasionally, for besides HEUSINGER's case in the Fowl already quoted, I have myself found it as a separate centre of bone in a fledgling of *Muscicapa grisola* I have found it under very similar conditions in a large series of Gallinaceous Birds, but I have no evidence of its existence in Ratitæ [‡]

When my abstract of this paper was read and published[§] I advocated the view that this structure represented an intercalary metacarpal, though I was not then aware that the same theory had been advanced before. But I am disinclined to urge the same view now. The late development of the part, its failure usually to form an independent osseous centre, its close association with the tendon of a certain muscle, its absence in Ratitæ, above all the want of any indication in near Reptilian allies of such an aborted digit, stand in the way of accepting or repeating my theory of a year ago.

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[*] "Beitrag zur Metamorphose des Vogel-Flugels," MECKEL's 'Archiv,' vol. 6, 1820, p 546. See also *ibid.*, vol 7, p 189

[†] According to SELENKA, in *Caprimulgus, Larus, Sterna, Phaëthon* (BRONN, vol 6, p 76), see Note to p. 394

[‡] I see no trace of it in MARSH's figure of *Apatornis*, the only Odontornith in which the metacarpus is well known.

[§] 'Roy Soc. Proc ,' vol 42, 1887, p. 52 ; 'Nature,' Feb. 3, 1887.

Two other vestigial structures attract attention. About the same time as the last-named rudiment appears, that is to say, about the tenth day, there is seen on the radial side of the base of the first metacarpal a piece of rather solid fibro-cartilage, which afterwards further solidifies into an arcuate nodule (*mc.*$^{1'}$). At the time of hatching it is still distinct and somewhat larger, and even in the Chick of six weeks old it is recognisable, but, thereafter, it fuses with the metacarpal of the pollex, helping to form its tubercle on the radial side.* This apophysis, which occupies the position of the spur† that so many Birds possess on the radial side of the wrist, may possibly be a surviving remnant of a pre-pollex It is very constant in all the Gallinaceous Birds that I have studied, but I have not found it yet among the Ratitæ.

A third remnant appears also about the tenth day on the ulnar side of the base of the metacarpal, and towards the flexor side of the manus (*mc.*$^{3'}$) It lies nearly opposite the junction of the carpal and metacarpal, and is about two-thirds as long as the accessory cartilage already described on the ulnar side of the index, it consists of hyaline cartilage. On the twelfth day (figs. 5, 6) it is twice as large as on the tenth, and in shape is flattish, sublanceate, but with a broader part below. It remains perfectly distinct through all the stages of incubation. In the Chick of a month old it is still obvious, but seems to be rotating slightly towards the flexor side, towards the angle of junction of the second and third metacarpals.

This cartilage, which is very distinct, constant, and well defined, and which does not appear to be in close relation with the origin or insertion of any particular muscle, may fairly, I think, be taken as the remnant of the next missing digit on the ulnar side.‡ I find it as a separate style of bone in the Toucan, and as a bony bridge in the Cariama.

Heusinger (*loc. cit.*) also describes a rudimentary fourth metacarpal, but the process supposed by him to be of that nature seems rather to be the one that I have shown to represent the third distal *carpale*.

The Phalanges.

Further, I have carefully examined the developing digits of many Chicks, especially among the Gallinæ and Ratitæ, with the object of reviewing the number of phalanges present either in a perfect state or rudimentary, and also to determine the presence or absence of rudimentary claws on other digits besides the pollex *

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* For the insertion chiefly of the *supinator longus*

† [illegible] developed in the Palamedeæ, certain Geese, Plovers, and Jacanas

‡ [illegible] found evidence of an additional (fourth) metacarpal on the ulnar side. also [illegible] Orn. Club [illegible] vol. 6, p. 6, 1881.

In many Birds, *e g* . the Passerinæ, the pollex of the first digit has only one phalanx attached to its short metacarpal, the second has two, and the third only one phalanx In others, *e g*, Plovers, Gulls, Cormorants, &c., an additional or ungual phalanx is found on the first and second digits, and in some Birds, *e g.*, *Numenius*, during the embryonic state, a small semi-distinct nucleus is seen on the end of the aborted phalanx of the third digit † According to current statements of authors, a nail or claw is frequently found on the thumb, on the index occasionally, but on the third digit never. Selenka ascribes a claw on the second phalanx of the pollex to most Gallinæ, many Raptores, Grallatores, and Natatores, *Hirundo*,‡ and others Nitzsch says it is absent in the Owls, very large in *Vultur* (*Neophron*) *percnopterus*, large in the Crane, short and bent in the Stork, thinner and longer in the Herons, but absent in the smaller Egrets, present in the Solan Goose, smaller and inconstant in the Gulls and Terns. The index claw is said to exist in most Ratitæ (*Casuarius* [Peron], *Rhea* [Nitzsch], *Struthio* [Perrault], *Apteryx* [Owen]), and in *Palamedea cornuta*. I find an embryonic claw on the index finger in all the Gallinaceous Birds that I have examined, and in *Dromæus*, as well as in the Ratitæ above-named And I find both in the young Ostrich and in *Rhea*, a small claw upon the end of the third digit

In the seven-day* Chick the diminutive fingers, formed of small, round, scarcely chondrified phalanges, are surrounded by a common web, and are all turned inwards, or towards the radial side. A notch separates the pollex from the second digit. On careful manipulation, we can see in the pollex *two* phalanges (Plate 62, fig 1, *dg.*^{1}, *dg* ^{2}), *three* in the second digit, and *two* in the third, and these numbers are not exceeded in the wing of any kind of adult Bird

By the eighth day the distal phalanx of the third digit has already disappeared by fusion with the proximal one; the distal phalanx of the second digit is indistinct; but that of the pollex is plainer than before.

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* The number of phalanges is always understated in the text-books Wiedersheim ('Lehrbuch,' p 195) says, "Die Phalangenzahl ist eine sehr beschrankte, indem dem ersten und dritten Finger je nur eine, am zweiten zwei vorhanden sind" And the same author says elsewhere ('Biolog Centralbl', vol 3, p 656, 1884), "Die Zahl der Fingerglieder ist eine sehr beschrankte, indem *schon im Fœtus* am ersten und dritten Finger je nur eine, am zweiten nur zwei zur Anlage kommen, und auch spater in derselben Zahl persistiren!" Owen ('Comp Anat') gives a similar account of the general condition, but describes the Ostrich correctly as an exception Stannius ('Lehrbuch,' pp. 259, 260) mentions the occasional presence of a second phalanx in the pollex, and a third in the index, but without specifying instances (*Cf* Nitzsch, 'Osteogr Beitr.', p. 89) Selenka (Bronn, vol 6, p 75, 1869) states that a second phalanx occurs in the pollex of Diurnal Raptores, Gallinaceæ, most Grallatores and Natatores, and *Cypselus;* and a third in the index of *Anser*, *Cygnus*, *Anas*, *Mergus*, *Colymbus*, *Scolopax*, *Grus*, *Struthio* Alix mentions a third phalanx in the index of the Tinamou ('App. locom'., p. 323)

† Bronn, 'Klassen u Ordnungen,' vol 6, p. 75

‡ This statement appears to be copied from Nitzsch, 'Osteographische Beiträge,' 1811, "Ueber das Nagelglied der Flugelfinger," pp 98–97, and *Hirundo* is a mistake of the transcriber for *Cypselus*.

On the tenth day the pollex is still larger proportionately than in its adult condition. The proximal joint has a thick shoulder like its own metacarpal, to which it is hinged by a very perfect condyle , its middle third (or nearly) has a long shaft The distal joint is no longer a flat sub-discoid part, but is a long and slender *claw core*, one-third as long as the proximal joint; it is beginning to be covered with horn. The first of the three phalanges of the second digit is very thick at its radial edge, and is bevelled at its ulnar, which is somewhat notched to receive the third digit.* The terminal phalanx is a small curved segment, ready to become the core of a claw.

The proximal phalanx of the third digit is one-half the length and one-third the width of that of the second.

On the twelfth day the claw-segment of the pollex is not so well developed, and that of the index is indistinct.

Passing to the young Fowl, three-quarters of a year old (fig 12), we find the distal phalanx of the pollex now forming the bony core of a claw. That of the index is a mere rough point, without a separate bony centre, and that of the third digit has disappeared.

In the Partridge, on the fourth or fifth day of incubation, a claw is also to be seen on the distal phalanx of the pollex, which, however, is unossified.

In the ripe embryo of the Quail, the claw of the pollex is distinct; the distal phalanx of the index is scarcely separate; and the third digit has only a single phalanx.

In a ripe embryo of *Gallus Sonneratii*, the distal phalanx of the pollex is a well-developed ungual hook, with a horny sheath or claw.

In the Turkey (embryo, half ripe), the distal segment of the pollex has a spatulate form, which form in *Phasianus versicolor* (two-fifths ripe) (Plate 63, figs. 4, 5) appears as a sub-circular disc In the latter species, the distal segment of the second digit also is an oval flat plate of cartilage This state of things, with more or less dilatation of the distal segment *before* the nail-sheath is developed, is constant in the Carinatæ.

In the Silver Pheasant (Plate 64, fig. 1), the claw on the pollex is not formed at the time of hatching, nor are the distal segments distinct in the other digits.

Metacarpus and Phalanges in Ratitæ.

Of all existing Ratitæ the wing is most degraded in the Emeu, which in this respect approaches most nearly to the recently extinct *Dinornis*, in which no trace of a wing has yet been found In a six weeks old Emeu chick the first metacarpal is about half the length of the second, and ends close to it in a point, the index finger possesses the normal number of phalanges, namely three, the last of which is enclosed in a sharp and curved claw In the old bird (Plate 65, fig. 4) the three phalanges and claw of the index are still distinct, but the metacarpal of the first is very small, and that of the third is suppressed The wings of an adult are about the size of those of a Jay or a Bower-bird, in the young chick, with legs the size of those of a Turkey, the wings are no larger than a Wren's.

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* I have more recently found that in some Birds, at least in the Gulls, Auks, and Guillemots, this flattened portion on the ulnar side of the first phalanx of the index, to which some of the primary quills are attached, does develop from a distinct tract of true cartilage It soon loses its independence (See 'Roy. Soc. Proc.,' vol. 43, 1888, pp. 322–325; and 'Nature,' Feb 2, 1888.) (*Cf supra*, p. 391) I have also shown that in long-winged Birds an additional accessory cartilage is present near the *ulnar side* of both the first and second digits, near their end. In that paper, p. 323, line 16 from the top, for "arm" read "also"; and p. 324, line 4 from the top, for "*policephala*" read "*poliocephala.*"

In the Cassowary (*Casuarius galeatus*), Plate 65, fig. 6) there is an evident third metacarpal fused with the second and first, and larger even than the second, the three rays being marked off by fissures. More perfect than the Emeu in this, it is yet less perfect in having only two phalanges in the index, of which the distal one is covered with a strong claw, curving towards the ulnar side *

In *Apteryx Owenii* (Plate 65, fig 5) the first metacarpal, less than half the size of the second, ends in a free point, as in the Emeu. Near the distal end, on the ulnar side, the large second metacarpal has a thin flange, which may be the masked rudiment of the third—a condition very different from that which we have just seen in the Cassowary. The index finger has *only* two short phalanges, and the falcate distal one bears a sharp curved claw

In the Hunterian preparation of a young Ostrich's wing already referred to (Plate 64, fig 12), the pollex has two phalanges, the index three, and the third digit two,† a number very uncommon among the Carinatæ. *Each digit possesses a claw*, that of the third digit being very small.‡

In *Rhea* (Plate 65, fig. 1) the first metacarpal is one-third, and the third almost three-fourths, the length of the second The third metacarpal extends beyond the second, as in Carinatæ The first digit only is perfect in the adult, and has a well-formed claw The second has two phalanges, of which the first has the usual flange on the ulnar side, and the second has a small claw. Inside the claw there probably was in the embryo the normal third phalanx. The third digit has one phalanx, flat and twisted; also a very small claw, in which doubtless the embryo had a second phalanx.

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* D'ALTON ('Skel d. straussartig Vogel,' 1827, p 17), MERREM ('Abh d Berliner Akad,' 1816–17, p 179), and MECKEL ('Archiv,' vol 13, p 231) give the same number of phalanges for the Indian Cassowary, and all agree in finding no trace of the first and third digits. Recently, however, I have dissected and figured the wing of a ripe embryo of *Casuarius Bennettii*, and find, besides two proximal and one distal carpal—the latter *in three lobes*, a small first metacarpal and a larger third metacarpal, and *three* phalanges attached to the large second metacarpal

† These two phalanges in the third digit of the adult bird are recorded by ALIX ('Appareil locomoteur,' p 323) See also the same author's "App locom de l'Autruche d'Afrique," 'Bull de la Soc Philomath,' 1867. OWEN describes the same number of phalanges in the young bird, probably from the same specimen ('Comp Anat.,' vol 2, p 73), but overlooks the claw of the third digit.

‡ Neither NITZSCH nor HUXLEY admits more than two claws. The cartilage may grow beyond the second bony phalanx in the third digit (see WRAY, 'Zool. Soc. Proc,' 1887, pp. 283–284, fig 1)

LIST OF ABBREVIATIONS.

c u	Centralo-ulnare.
d.c.^{1}	First or radial distal *carpale.*
d.c.^{2}	Second distal carpale.
d.c.^{3}	Third distal carpale.
dg ^{1}	First or proximal phalanx.
dg.^{2}	Second phalanx.
dg.^{3}	Third phalanx.
h.	Humerus.
i.r.	Intermedio-radiale.
mc.^{1}	First metacarpal, or metacarpus pollicis
mc.$^{1'}$	Accessory cartilage of ditto (pre-pollex ?).
mc.^{2}	Second metacarpal, or metacarpus indicis.
mc.$^{2'}$	Accessory cartilage of ditto.
mc.^{3}	Third metacarpal.
mc.$^{3'}$	Accessory cartilage, probably a rudimentary fourth metacarpal.
r.	Radius.
rd.	Radiale.
u.	Ulna.
ul.	Ulnare.

DESCRIPTION OF THE PLATES

N.B.—Figs 7–10 of Plate 65 will be described in a future paper, the whole of this piece of research is referred to in the "Abstract" ('Roy Soc. Proc,' vol. 42, pp. 52–58*), but only part is given in the present paper.

Plate	Fig.	*	Number of times magnified.
62	1	Wing of Chick, 7 days' incubation, outer view	13$\frac{2}{3}$
,,	1A	Part of same; inner view	13$\frac{2}{3}$
,,	2	The same; 8 days' incubation, outer view	13$\frac{2}{3}$
,,	3	The same, 10 days' incubation; inner view	8
,,	4	Part of same; outer view	12
,,	5	The same; 12 days' incubation; outer view	8
,,	6	Part of same; inner view	12
,,	7	The same; 2 weeks' incubation; outer view	6$\frac{2}{3}$
,,	8	Part of same; inner view	10
,,	9	The same; 2 or 3 days old; inner view	5$\frac{1}{3}$
,,	10	The same; 33 days old; inner view	2$\frac{2}{3}$
,,	11	The same; 6 weeks old; inner view	2$\frac{2}{3}$
,,	12	Wing of young Fowl, $\frac{3}{4}$ year old; outer view	nat. size.
63	1	Part of wing of young Fowl; $\frac{3}{4}$ year old, inner view	nat. size
,,	2	Do. of old Hen; outer view	nat. size.
,,	3	Part of same; inner view	nat size.
,,	4	Wing of *Phasianus versicolor*; $\frac{2}{5}$ ripe; outer view	8
,,	5	Part of same; inner view	8
,,	6	Wing of same species; nearly ripe; outer view	5$\frac{1}{3}$
,,	7	Part of same; inner view	5$\frac{1}{3}$
,,	8	Part of same; inner view	21
,,	9	Wing of *Argus giganteus*; ripe; inner view	4
,,	10	Part of same; outer view	6
,,	11	Wing of *Euplocamus Horsfieldii*; inner view	5$\frac{1}{3}$
,,	12	Part of same; outer view	8
,,	13	Wing of *Euplocamus melanotis*; $\frac{2}{3}$ ripe; inner view	6$\frac{2}{3}$

* P 58, line 11 from bottom, *for* "*always*" *read* "*never*, so far as I know"

Plate	Fig		Number of times magnified
64	1	Wing of *Nycthemerus argentatus;* ripe, outer view	$5\frac{1}{3}$
,,	2	Part of same, inner view	$5\frac{1}{3}$
,,	3	Part of same, inner view	21
,,	4	Wing of *Lophophorus impeyanus;* ripe; inner view .	$5\frac{1}{3}$
,,	5	Wing of *Perdix cinerea;* 1 week old; outer view.	4
,,	6	Wing of *Coturnix dactylisonans*, ripe; inner view .	$6\frac{2}{3}$
,,	7	Part of same, outer view	$6\frac{2}{3}$
,,	8	Wing of *Meleagris gallo-pavo;* ½ ripe, outer view	$6\frac{2}{3}$
,,	9	Part of same, inner view	$6\frac{2}{3}$
,,	10	Wing of *Gallus Sonneratii;* ripe; inner view . . .	$6\frac{2}{3}$
,,	11	Part of same, outer view	10
,,	12	Wing of *Struthio camelus;* ½ grown; outer view . .	nat. size.
,,	13	Part of 3rd digit of same	4
65	1	Wing of *Rhea americana;* adult; inner view . . .	nat. size.
,,	2	End of 2nd digit of same	4
,,	3	Part of 3rd digit of same	4
,,	4	Wing of *Dromæus ater;* adult; outer view . . .	⅔ nat. size
,,	5	Wing of *Apteryx Owenii;* adult; outer view . . .	4
,,	6	Wing of *Casuarius galeatus;* adult, outer view . .	nat. size.
,,	7	Palate, partly dissected, of *Dromæus irroratus;* nearly ripe	nat size.
,,	8	Pelvis of embryo of *Casuarius Bennettii;* lower view .	$1\frac{1}{3}$ nat. size
,,	9	The same, upper view	$1\frac{1}{3}$ nat. size.
,,	10	The same, side view	$1\frac{1}{3}$ nat. size

XV. *The Electric Organ of the Skate.*

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Communicated by Professor J. BURDON SANDERSON, *F.R.S.*

On the Development of the Electric Organ of Raia batis.

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[PLATES 66, 67.]

THERE are few, if any, structures in the animal kingdom the origin of which is more difficult to account for than the electric organs of Fishes. DARWIN recognised in the electric organs one of the "special difficulties of the Theory of Natural Selection,"* and, although we now understand their structure and development, it is still "impossible to conceive by what steps these wondrous organs have been produced." Although the structure and development of the electric organ of the Torpedo has been determined, we are as ignorant as before of its phylogeny.

Almost the only chance of our obtaining a hint as to how the organ passed through its initial stages, as to the causes which were at work while the muscular fibres were in process of conversion into electric cells or discs, seems to be by turning to the so-called "pseudo-electric"† organ of the Skate.

The organ of the Skate has hitherto received comparatively little attention from biologists. We are mainly indebted for what we know of its structure to ROBIN,‡ while the limited information we possess as to its development is entirely due to the inquiries of BABUCHIN.

In turning to the common Gray Skate (*Raia batis*), one is at once struck with the remarkable fact that, while the organ has not yet been proved to have any special use, it is apparently as structurally perfect as the organ of the Torpedo. The presence of an extremely complex apparatus, having no evident function, is difficult to understand; and, before venturing any explanation of this unusual circumstance, it is desirable, if possible, to enquire whether the organ of the Skate is on the up or the down grade—whether, having reached a high state of elaboration, it is now increasing in functional importance, or whether, its days of usefulness being over, it is slowly undergoing retrogressive changes.

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* 'Origin of Species,' 6th edit., p. 150.

† "Pseudoëlektrisches Organ bei einem Gymnotinen?" 'Untersuchungen am Zitteraal, *Gymnotus electricus*,' von DU BOIS-REYMOND, Leipzig, 1881, p. 66.

‡ 'Ann. Sci. Nat.' (*Zool.*), vol. 7, 1847, p. 193.

To determine the present condition of the Skate's organ is by no means a simple matter. To start with, it is desirable to make out not only its development, but also the period at which it first appears, the rate at which development proceeds, and the changes, if any, which set in after development has been completed. Further, it will be equally necessary to make a comparative study of the organ in the various members of the Skate family. Having, through the kindness of Professor BURDON SANDERSON, had the opportunity of making a very complete examination of the electric organ of the Torpedo, I was able some time ago to direct my attention to the organ of the Skate, with a sufficient appreciation of the difficulties to be overcome and of the points which deserved especial attention.

With a view to arriving at some general conclusions as soon as possible, I first, with the help of one of my assistants (Mr G. C. PURVIS, M B), made a preliminary examination of the electric organ at various stages of development in eight different species of Skate. This done, I next proceeded to make as thorough an investigation as possible of the development of the organ of the Gray Skate (*R. batis*). Before referring at length to the comparative anatomy of the organ in the various members of the genus *Raia*, I have thought it desirable to prepare a paper dealing almost exclusively with its development in *Raia batis*. I have already ascertained that there is considerable diversity in the time of appearance and development of the organ in the Skate genus, as well as a marked difference in its form and structure. In the Gray Skate, as is well known, the organ consists of numerous discs, but in some other forms (*e g*, *R radiata*), instead of large complex discs, we have small simple cup-shaped bodies provided with long or short striated tails, each cup being lined with an enlarged motor (electric) plate, and coated with a richly nucleated layer of protoplasm. The form and character of these cup-shaped organs seem to indicate that they have been retarded in their development, but the question still remains—Are they advancing or receding? Are these electric cups degenerated discs, or are they the primitive ancestral elements out of which the discs have been evolved? Do these characteristic cups ever develop into discs, or do they, after having persisted for a time, finally disappear, or are they distinct and independent structures?

These and various other questions at once suggest themselves for solution, but in the meantime I need only say that I believe the large discs of the common Skate have been derived from cup-shaped structures, such as still persist in certain adult forms—that, in fact, the electric plate of the disc in *Raia batis* is the greatly expanded lining of a simple cup-shaped structure, such as exists in *Raia radiata*, while the accessory portions of the disc have been derived from the muscular substance composing the body of the cup.

To make the account of the development intelligible it will be desirable to shortly describe the structure of the hitherto imperfectly described organ of the Gray Skate. While in the Torpedo the electric elements are arranged to form numerous vertical columns, in the Skate they give rise to numerous hollow cones, which are fitted within each other to form two elongated electric spindles, one at each side of the tail.

Each of the discs of which the electric cones of the Gray Skate are composed consists essentially of three distinct layers, exclusive of the nerves and vessels distributed to it and the connective tissue in which they are embedded. The first layer, beginning from the anterior side, may be known as the electric plate, which consists of a layer of protoplasm, containing large nuclei (*a*, figs 10 and 13). Extending to end in this plate (which probably corresponds to the motor plate of muscles) are numerous nerves (*g.*, fig 13) which divide dichotomously as they pass backwards through a supporting connective tissue framework.

The second layer may be known as the striated or meandriform layer (*b.*, figs. 8, 10, and 13). It consists of a compact mass of lamellæ, which, though they often present an extremely sinuous appearance, are seemingly continuous from one end of the disc to the other This striated layer is easily separated from the electric plate in front, and it can also, though less readily, be detached from the third layer lying immediately behind it. This third layer may be known as the alveolar layer (*c*, figs 10 to 13). Its anterior surface is smooth and even, while the posterior is extremely irregular, and presents a number of spaces or alveoli (figs. 11 and 12) which somewhat resemble the sacculations in a Frog's lung. From this alveolar layer a funnel-shaped projection (*d.*, fig. 13), which ends in a long narrow process, is sometimes seen extending obliquely backwards.

Behind these three layers, which form the disc proper, there is a thick cushion of gelatinous tissue (*f*, fig. 13), which fills up the space between the alveolar layer and the septum (*s*, fig 13) that forms the posterior wall of the chamber in which the disc lies.

Enclosing the disc, with its nervous layer in front and the gelatinous cushion behind, there is a complete fibrous investment, which is continuous with the fibrous septa that lie between the adjacent discs and the connective tissue that lies between the electric cones. Each disc (when the nerves and gelatinous tissue are included) may hence be said to lie in a cell or chamber, to the walls of which it is chiefly attached by the nerves and their accompanying connective tissue fibres in front, and by the blood-vessels which enter the chambers from behind

From a general consideration of the electric organs of the Torpedo and Gray Skate, it seems evident that the essential structure is the electric plate, and that, in order to have an efficient organ it is necessary to provide a large superficial area for the terminations of an incalculable number of nerve fibres

This is gained with the greatest economy of space when numerous small insulated plates are piled above or in front of each other, and held in position by a delicate framework. A structural homologue of the electric plate on a small scale already exists in the motor plate of muscles. In the production of the electric organ of the

Skate advantage has been taken of this already existing structure, which has been in fact enlarged to form the essential part of the organ, while the muscular fibre to which the motor plate belonged has been utilised in the formation of certain accessory portions of the organ.

Previous to the researches of BABUCHIN the development of electric organs was practically as obscure as their origin, and even now many biologists are unable to understand the relation between muscular fibres and electric columns and discs. BABUCHIN, in addition to working out the development of the Torpedo organ, has on several occasions referred to the organ of the Skate. The material at his command, however, seems to have been limited, and it was impossible to identify the species of some of the embryos examined. From the figures accompanying BABUCHIN'S most important paper, it is probable that his observations were made, in part at least, on the Flapper Skate (*Raia macrorhynchus*). Apparently, neither *R. batis* nor any of the forms having cup-shaped organs were subjected to examination. BABUCHIN* describes the now familiar "clubs," and refers to the more important stages of development, including the formation of the alveolar and striated layers; but his clubs seem to have passed directly into flattened discs, and the stems or processes were not found after the Skate had reached a length of 15 cm.

While in the Torpedo the electric organ appears at a very early stage of development, and begins to discharge feeble shocks before the young escape from the oviduct, in the Skate the rudiments of the organ are late in appearing, and development is, in some cases, extremely slow.

In very young embryos of *R. batis* there is no indication of an electric organ, the position of the organ being occupied by unaltered muscular fibres; but in an embryo about 7 cm. in length the rudiments of the future organ are easily recognised, both in teased preparations and sections.

I have figured the embryo (Plate 66, fig. 1) in which the earlier stages were studied, so that the period of development may be the better understood. It will be observed that the so-called external gills (fig. 1, *g*) still persist, and that the tail is relatively long and powerful. The large yolk sac is not represented in the figure.

In this embryo the rudiments of the organ were in the form of long slender clubs (fig. 2) which occupied the vertebral or inner portion of the muscular band lying next the notochord. In transverse sections through the middle of the tail, where the clubs are most numerous and most advanced, they are seen to be few in number and to occupy a very small and indistinctly defined area, being still surrounded, except on the side adjoining the notochord, by unaltered muscular fibres. Transverse sections are, however, especially interesting in demonstrating the existence of muscle nuclei in the substance of the head of each club and between the head and the sarcolemma, and in showing a marked increase of embryonic connective tissue cells between and around the various clubs. They also in some cases point to the existence of a channel at or near the centre of the stem of the club, which may have resulted from the migration forwards of the muscle nuclei. In longitudinal sections (fig. 2) the gradual change from an ordinary muscular fibre to an electric club can easily be traced

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* For titles of BABUCHIN'S papers see p. 407.

The anterior end of the muscular fibre destined to become a club assumes a rounded form, and the nerve and the motor plate become more distinct, and the muscle nuclei increase in number. As the muscle nuclei increase the head expands and retreats slightly from the septum to which it was originally connected, leaving the intermuscular tissue in the form of a funnel-shaped expansion, within which lie the now enlarged nerve fibre and a number of round and oval embryonic connective tissue corpuscles These corpuscles gradually increase in number, and eventually form the connective tissue framework which supports the numerous branches of the nerves proceeding to the electric plate. Had there been no interference with the muscular fibres, the muscle nuclei would have ministered to their growth, and probably also to a certain extent to the enlargement of the motor plate. The energy of these nuclei is, however, now largely diverted into new channels; for, while some continue, evidently under unfavourable conditions, to increase the size of the muscular fibre, the greater number migrate in one of two directions—forwards, to assist in enormously increasing the motor plate, or, outwards, to give rise later to the alveolar layer. *They all, however, seem to remain within the original sarcolemma.*

The clubs (as fig. 2 indicates) usually make their appearance from within outwards; but, however they appear, some of them are further advanced than others, and the precedence at first gained is maintained throughout the whole period of development. In somewhat older embryos clubs are found at one part and rudiments of discs at another. Figs. 3, 4, 5, and 6 are all taken from one section from near the centre of the tail of a Skate about 10 cm. in length. The great difference in the size and elaboration of the clubs at the same part of the tail is worthy of special note.

As the size of the head of the club increases the development of the stem is arrested, and after a time the whole club, instead of being as long as the adjacent muscular fibres, is at least one-third shorter; and as development proceeds, the tail or process is reduced to a long, narrow, somewhat ribbon-shaped structure, only partially striated (figs 3 to 9)

It may hence be taken for granted that the expansion of the anterior end of the original muscular fibre has resulted from a change in the motor plate, accompanied by corresponding changes in the motor nerves and the cells in the spinal cord from which they originate. This seems to be corroborated by the fact that in slightly older embryos the nerve cells around the embryonic neural tube are relatively large and distinct.

As the motor plate, with the help of the rapidly multiplying muscle nuclei (which continue to arrive for some time from the head of the club), increases in size the nerves in connection with the plate develop new branches, which occupy a nearly vertical position in front of the plate. These branches, after reaching a certain size, are provided with a sheath and held in position by the connective tissue network already referred to

Coincident with the increase of the motor plate there is an enlargement of the head of the club, which gradually loses its rounded form and assumes a truncated appearance, somewhat resembling a mace. In front of the flattened anterior surface of the mace there lies the richly nucleated motor plate. When this stage has been reached the striation of the anterior portion of the mace is observed to be much closer than that of the posterior portion, while at the root of the stem the striation has almost completely vanished.

There is, further, a diminution of the muscle nuclei in the anterior portion, and an increase in and around the posterior portion, of the head of the mace; and in many cases the head of the mace is tilted so as to form an obtuse angle with the stem

The next stage is an exceedingly important one. The front portion of the head of the mace, in order to support the ever-increasing motor plate (which may henceforth be spoken of as the electric plate), expands transversely, and at the same time projects the whole, or the greater portion, of its margin forwards, and thus forms an extremely shallow cup-shaped structure, which is, of course, lined by the electric plate.

The finely striated anterior portion of the mace is chiefly involved in the formation of this electric cup. The beginning of the cup is indicated in fig. 3, and later stages are represented in figs. 4 and 5.

As the expansion and moulding take place the few nuclei which persist in the striated front part of the mace either pass forwards into the electric plate, backwards towards the unstriated portion, or they disappear; and when all these nuclei have vanished the finely striated portion of the mace has, without any marked change, become the striated layer, while the nuclei behind this layer arrange themselves to form the rudiment of the alveolar layer. The nuclei behind the striated layer very closely resemble the nuclei of the electric plate. They may both be considered muscle nuclei, which have entirely, or to a large extent, lost their muscle-forming properties. The striated layer, having been once established, remains, as far as I have observed, absolutely free of nuclei. We may suppose that it obtains the nourishment required for its further growth from the protoplasm lying in contact with one or both of its surfaces.

The cup stage having been reached, there is apparently a short pause, which is followed by a period of considerable activity in all the three layers.

The electric layer, at first quite within the margin of the shallow cup, gradually increases until the edge is reached As this takes place the striated layer first increases in thickness and has its margins recurved. It then steadily expands to form the large characteristic striated layer of the fully developed disc. This layer is represented in figs. 4 to 13 (*b*). It is always distinctly striated; but its thickness and the amount of sinuosity of the lamellæ vary with the mode of preparation. In the completed disc the form of the striated layer varies considerably. In front views it presents sometimes a circular, sometimes a nearly hexagonal, outline In side views of the entire disc the margin is uniformly but unequally curved backwards, while in sections it appears sometimes distinctly concave in front, at other times convex—or it may be concavo-convex, the form again partly depending on the mode of preservation.

The alveolar layer may next be considered. It is at first represented by a nucleated layer of protoplasm lying between the posterior surface of the striated layer and the sarcolemma at the base of the mace. The nuclei multiply, and protoplasmic projections, containing one or more nuclei, begin to grow backwards around the stem of the mace or cup (fig. 6). These projections vary greatly in form; some of them are long and rounded, but in most cases they consist of relatively broad flattened processes, which, as they grow backwards, give rise to irregular pit-like depressions

As the original processes increase in length they throw out lateral projections, which, by meeting and fusing with each other, give rise to an irregular network (figs. 7 and 9). By the appearance of still more delicate processes, a fine network is formed within the larger pits immediately behind the striated layer.

These processes and pits are represented in figs 7, 8, 9, and 10, and the network formed by their fusion is shown in figs. 11 and 12. The nuclei of this alveolar layer are from the first large and prominent, and as development proceeds they are surrounded by a clear area of unstainable protoplasm, which in some cases (*h*. fig. 10) reaches a considerable thickness. After a time the nuclei and the surrounding protoplasm are less distinct. In longitudinal sections of the alveolar layer (figs. 10 and 13) the most striking objects are the prong-like backward extensions of the original simple processes

Having considered the striated and alveolar layers, the electric plate may now be further described. During the club and mace stages the electric plate consists of a layer of protoplasm, which is almost obscured by the numerous large nuclei embedded in its substance (figs 4, 5, and 6). After a time the multiplication of the nuclei seems to come to an end; hence, as the plate increases, they are gradually separated from each other. Fig. 8 indicates the arrangement in a Skate 20 cm. in length, and fig. 10 the relative proportion of nuclei to protoplasm in a Skate 25 cm in length In the last-mentioned Skate, the electric plate was extremely distinct and relatively thicker than at later stages, in which the nuclei are flattened and apparently applied to the surface of the striated layer, while the protoplasm in which the nuclei are imbedded is reduced to a thin and nearly transparent membrane. As figs. 10 and 13 indicate, the electric plate lies in contact with the striated layer, but is not inseparably connected with it, while it becomes continuous with the alveolar layer round the margin of the disc. On the anterior surface of the electric plate there is a delicate nerve plexus (fig. 10, *g*.); but no fibres appear to pass through its substance, either in a vertical or oblique direction.

The general arrangement of the nerve fibres which pass to the electric plate is indicated in fig. 13. It will be observed that to a large extent they lie at nearly right angles to the electric plate, and that they branch dichotomously as they proceed to end in its substance.

Having considered the structures directly or indirectly derived from the head of the original club, we may now refer further to its shaft or stem. This at first is distinctly striated; but as the condensation takes place in the club or mace to give rise to the striated layer, the transverse markings at the base of the stem disappear, and this part of the stem undergoes vacuolation, only a few clear oval corpuscles remaining in contact with the sarcolemma. As the anterior third of the stem is altered the communication between the posterior portion and the developing disc seems to be cut off (figs. 3 to 9); and occasionally, immediately behind the atrophied portion, there is, as it were, a whole detachment of muscle nuclei arrested in their attempt to move forwards to take part in the formation of the disc. The muscle nuclei left in the posterior portion of the stem continue in a feeble way to produce muscular tissue; but they only succeed in forming a long, slender, and apparently useless process.

This process, however, long retains its striated appearance; and, although it has not hitherto been detected in a Skate over 15 cm. in length (and its existence in a fish of this size seems to have surprised BABUCHIN), I have had no difficulty in finding it practically unaltered in Skates over 60 cm., and on several occasions I have found it both in sections and in teased preparations of discs from fully developed organs. I ought to add that the terminal portion of the stem is often enlarged and crowded with nuclei; whether the stem always ultimately disappears has not yet been determined. It is not surprising that it is seldom seen in sections, for it is eventually reduced to form a thin ribbon, which, unless the section runs parallel with its long axis, easily escapes detection; and, further, it gets deeply embedded in the connective tissue framework and is easily obscured by the accompanying blood vessels and nerves. It will be observed in fig. 13 that the stem springs from a funnel-like expansion attached to the under surface of the disc This funnel consists partly of the remains of the head of the original club, or rather of the electric cup, and partly of the dilated base of the stem—the dilatation having taken place as the cup gradually expanded to form the relatively large flattened disc. In some cases, when there are long projections from the alveolar layer, one or more of them may simulate the stem of the original club; while, on the other hand, when only a short portion of the stem is left in the section it may be mistaken for one of the projections from the alveolar layer.

In concluding the description of the electric disc, it is only necessary to add that there are discs at several stages of development and growth in the same part of the tail, and that the discs continue to enlarge as the fish increases in size. But apparently the organ becomes active (*i.e.*, acquires the power of discharging electric shocks) long before the maximum size is reached, for I understand SANDERSON and

GOTCH* have obtained decided shocks from Skates considerably under 60 cm. in length.

The thick layer of connective tissue which lies behind the alveolar layer is represented in fig. 13 (*f.f.*), which also indicates the connective tissue investment of the entire electric cell or chamber and the connective tissue septa (*s*) which lie between the various chambers The walls of the chambers are largely derived from the original septa (*s.*, fig. 2), which lie between the myotomes, while the thick layer of tissue behind the alveolar layer is derived from the embryonic connective tissue corpuscles which are so extremely abundant around the clubs and rudimentary discs.

In another communication I hope to give an account of the structure of the cup-shaped bodies of which the electric organ of *Raia circularis* and other forms is composed.

LITERATURE.

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Ubersicht der neuen Untersuchungen uber Entwicklung, Bau, und physiologische Verhaltnisse der elektrischen und pseudoelektrischen Organe; von A. BABUCHIN. Archiv für Anatomie und Physiologie, 1876.

EXPLANATION OF PLATES.

PLATE 66.

Fig. 1. Dorsal view of the smallest *R. batis* embryo in which the rudiments of the electric organ were observed. The large yolk bag is not represented. *g.* So-called external gills. Natural size.

Fig. 2. Longitudinal horizontal section through the tail of the embryo figured (fig. 1), showing the muscular fibres developing into clubs.

1. and 2. Well-marked clubs, with numerous muscle nuclei lying in contact with the enlarged anterior end.

3. A club with a pit-like depression at free end, and nuclei apparently in the process of migrating from the interior of the altered muscular fibre.

4. A muscular fibre only very slightly altered, lying in contact with an ordinary muscular fibre.

Observe the oblique position of the clubs, that the muscular striations still persist, even at the expanded portions; note also the intermuscular septa. The connective tissue corpuscles, which are extremely numerous around the clubs, are scarcely represented.

ZEISS' apochromatic 4, eyepiece No. 3. Outlined with ZEISS' camera.

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* 'Journal of Physiology,' vol. 9, Nos. 2 and 3 (August, 1888).

Fig. 3. Two clubs from a slightly older Skate embryo (*R. batis*); one (1) a little more advanced than the other. both clubs are considerably larger than those represented in fig. 2.

a. The enlarged motor plate, with numerous nuclei embedded in its substance, and well-defined nerve fibres (*e.*) proceeding towards its anterior surface. Observe the nuclei in connection with the sheaths of the nerves, and the connective tissue corpuscles scattered amongst them.

b. The portion of the club which is altered to form the striated layer of the disc, behind which lie nuclei (*c*) which give rise to the alveolar layer.

d. The stem or tail of the club, which is still muscular.

Zeiss' apochromatic 4, eyepiece No 3. Outlined with Zeiss' camera

Fig. 4. An isolated club which has expanded to form a shallow electric cup Letters as in fig. 3.

Fig. 5. From a longitudinal section to show one of the first steps towards the formation of the electric disc Note that the three principal layers (*a.*, *b.*, *c.*) are already represented—the alveolar by a layer of richly nucleated protoplasm.

Figs. 4 and 5 drawn with Zeiss' apochromatic 4, eyepiece No. 3.

Fig. 6. A somewhat more advanced stage, more highly magnified (Zeiss' apochromatic 4, compensating eyepiece No. 12), showing (*a.*) the large nuclei of the electric plate; (*b.*) the striated layer; (*c.*) the alveolar layer, sending out blunt processes, and (*d.*) the long stem.

Drawn with Zeiss' camera.

The stages represented in figs. 3, 4, 5, and 6 were all present in the same Skate.

Fig. 7. Sketch of an isolated disc from a Skate nearly 60 cm. in length, showing the projections and alveoli of the alveolar layer, and the long stem, which still retains some of its striations. Letters as in fig. 6.

Zeiss' apochromatic 4, eyepiece No. 3.

PLATE 67.

Fig. 8. Longitudinal section through a disc, slightly larger than fig. 7, showing the nucleated electric plate (*a*); the processes of the alveolar layer (*c.*) extending into the posterior gelatinous cushion (*f.*); the connective tissue sheath (*s.*); and the long stem (*d.*) with a trumpet-like expansion (*e*) where it joins the disc.

Zeiss' apochromatic 4, eyepiece No. 3.

Fig. 9. Sketch of an isolated disc from the same Skate as figs. 7 and 8. Observe that (though the magnifying power is the same) it is larger than fig. 7. The alveolar layer (*c.*) is now extremely complex; the stem (*d.*, *e.*) is ribbon-shaped, but still striated posteriorly; and the electric plate presents a still larger area for the terminations of the electric nerves. *b.* Striated layer. *d* Electric plate.

Fig. 10 A portion of a disc from a slightly older Skate, magnified 950 diameters

a The electric plate with its large distinct nuclei, and a nerve plexus ? (*g.*)

b. The striated layer in the form of a narrow sinuous band.

c The alveolar layer with (*c.*′) simple and compound (*i.*, *d.*) projections, giving rise to primary and secondary alveoli. Note the large nuclei and the clear protoplasm (*h.*) surrounding them.

Zeiss' apochromatic 4, compensating eyepiece No 12. Drawn with Zeiss' camera.

Figs. 11 and 12. Two transverse sections through the alveolar layer of a fully developed disc. Fig. 11 shows the fine network formed by the processes of the alveolar layer immediately behind the striated layer, while fig 12 shows the wider network some distance from the striated layer. The spaces are occupied by gelatinous tissue, containing blood vessels.

Zeiss' AA, eyepiece No. 3.

Fig. 13. Longitudinal section through a disc from a Skate (*R. batis*) about 27 inches in length. This sketch illustrates the general structure of an electric disc in *Raia batis.* The blood vessels are not included.

g. The nerve fibres passing to the electric plate. The fibres, at first large and provided with a medullary sheath, divide dichotomously as they approach the plate, and eventually have only a gray sheath. They all terminate on the anterior surface of the plate, where they seem to form by their terminal divisions a series of delicate loops or rings. The spaces between the nerve fibres are occupied with gelatinous tissue, containing numerous nuclei.

a The electric plate, consisting of a layer of protoplasm capable of being divided into two lamellæ, the posterior of which contains large nuclei.

b. The striated layer, made up of numerous lamellæ having an exceedingly sinuous arrangement.

c. The alveolar layer, with processes projecting backwards into (*f.*) the gelatinous cushion, and connected together by secondary processes to form an irregular network

dd. The stem of the disc, which consists of the altered posterior portion of the original muscular fibre, part of which is still indistinctly striated (*e.*). The part of the stem surrounded by the projections of the alveolar layer is considerably dilated. This dilated portion, together with the upper half, or more, of the narrow portion, is embedded in the gelatinous tissue.

s. Septum between two electric chambers.

s′. Part of the original transverse intermuscular septum

On the Structure of the Electric Organ of Raia circularis.

Received April 30,– Read May 17, 1888.

[PLATE 68.]

IN the preceding paper " On the Development of the Electric Organ of *Raia batis*," I mentioned that in some Skates (*e.g*, *R. batis*) the electric organ consists of rows of discs, while in others it is made up of numerous small cup-shaped bodies. These electric cups (which, as far as I can ascertain, have never been observed before) I first noticed in *R. circularis*, but they are equally well marked in *R radiata* and *R fullonica.* In *R. radiata*, however, the electric organ is extremely small (while the individual cups seem to be incompletely developed); and, *R fullonica* being comparatively rare in our waters, I found it most convenient to study the structure of the cups in *R. circularis*.

This Skate sometimes reaches a length of 3 feet, and the tail is usually a little more than half the length of the entire fish. The dorsal aspect of the tail is studded with numerous large and small denticles, which, however, differ considerably in their distribution in different individuals.

The electric organ in *R. circularis* only occupies a relatively small portion of each side of the tail, in this respect differing decidedly from the organ of *R. batis*, which extends from the inner surface of the skin to the vertebral column, leaving a very small space for the posterior portions of the caudal muscles. Although the electric organ only occupies a small segment of the tail in *R. circularis*, it reaches a considerable length. In a specimen which was nearly 27 inches (68 cm.) in length from tip to tip, the electric organ measured 8¼ inches (21 cm.) in length, was 5 mm. in breadth, and nearly 25 mm. in thickness at the thickest central portion. This organ is represented, natural size, in Plate 68, fig. 1. When exposed, it was seen to occupy the posterior two-thirds of the tail, and the posterior portion (three-fifths) lay immediately under the skin, while the anterior portion (two-fifths) was embedded in the caudal muscles.

The exact position of the organ will be at once understood by a reference to fig. 2, which represents a transverse section through a portion of the tail, about 4 inches from its termination. It will be noticed that the nerve of the lateral line (*n.*, fig. 2) is in contact with the outer surface of the organ, and that the organ has a somewhat oval form in section.

When the organ is removed it has, owing to the tapering at the ends, a striking resemblance to a slightly flattened spindle (Plate 68, fig. 1). The posterior end, which reaches to the tip of the tail, is usually more pointed than the anterior end, which is enveloped by muscular fibres.

In thick transverse sections of the fresh organ it is possible to distinguish with the naked eye the nearly circular cups. These vary in number in the different sections, but they are always more abundant in the thick central portion of the organ than near the extremities. When slightly magnified (fig. 2, *c.c.*) the cups become more evident, and the nerve (*n.*) of the lateral line is seen indenting the outer surface.

Fig 2 also shows the relation of the organ to the skin and the caudal muscles, the outer surface is in contact with the subcutaneous tissue; the inner surface is separated from two well-marked muscular bands by a thick fibrous septum, from which an intermuscular septum projects inwards towards the vertebral column Along this transverse septum vessels and nerves find their way to the electric organ. Transverse sections made near the ends of the organ only differ from sections of the thick central part in the number of the cups, at the terminations only one or two cups may be found, but they are apparently as perfect as, though less regular in form than, the cups at the centre of the spindle.

The size and form of the cups can be readily determined by means of thick sections of the fresh organ, or by teasing portions of an organ which has been macerated in nitric acid. In teased preparations it is often possible to study completely isolated cups When a dozen or more cups are under observation, it is at once evident that, although they all resemble each other, there is over all a considerable amount of variation both in shape and size. Some of the cups are comparatively shallow, while others are both wide and deep, it is possible that the shallow ones only differ from the others in being less fully developed. One of the most regular and common forms is represented in fig. 3 It will be noted that this cup is of a considerable size, so large, in fact, that it does not necessarily follow, as I originally supposed when studying the organ of *R. radiata*, that organs made up of cups have been arrested in their development. In describing the development of the organ in *R. batis*, I mentioned that the discs passed through an indistinct cup stage, but the cup in *R. batis*, instead of becoming deeper, has its margin everted to form, first, a mushroom-shaped structure, and, eventually, a large flat disc.

In *R. circularis* and others, however, as will be afterwards described, exactly the opposite changes set in; the head of the original muscular club is moulded as it increases in size to form a thin-walled cup, from which the posterior part of the muscular fibre projects in the form of a long or short stem. At first one is apt to suppose the cups must be far less effective than the discs. Whether this is the case or not has still to be determined, but it does not necessarily follow; for, if the superficial area of such a cup as is represented in fig. 3 is compared with the superficial area of a disc from *R batis*, it will be found that the extent of the one nearly corresponds to that of the other. Owing to a given number of cups occupying a smaller space than a corresponding number of discs, it is conceivable that it might require an organ composed of discs to be somewhat larger than an organ composed of cups to be equally effective. As to the cups, I ought, perhaps, to mention that in transverse sections those near the periphery are often flattened and irregular. This irregularity is, however, in most cases due to the influence of reagents. In longitudinal sections (2A) the cups are seen to be arranged in oblique rows, so that the adjacent cups, to a certain extent, alternate with each other. This holds for both horizontal and vertical longitudinal sections. By this arrangement a large number of cups can be packed in a comparatively small space.

A reference to fig. 2A will also show that, though the individual cups are usually slightly tilted to one side, the wide open mouth, which always looks forward, is nearly at right angles to the long axis of the organ

In giving a short account of the discs of *R. batis* in the previous paper, I pointed out that each consisted of three essential layers, viz · (1) an electric plate, (2) a striated layer, and (3) an alveolar layer; and that a layer of gelatinous tissue supported the nerves in front, while a thick gelatinous cushion lay behind each disc, filling up the alveoli and forming a convenient stratum for the blood vessels. The advantage of recognising that each electric element consists of only three important layers becomes evident when the cup-type of electric organs is considered.

In *R circularis*, for example, each cup consists of (1) a thin lining, (2) a thick central layer, and (3) a dense cortex, invested with a thin coating of gelatinous tissue. The lining of the cup is practically identical with the electric plate of the disc of *R. batis;* the thick central layer corresponds to the striated layer of the disc, while the cortical layer represents the alveolar layer of the disc Corresponding to the nervous layer in *R. batis*, we have in *R. circularis* a bunch of ever-dividing nerve fibres, with gelatinous tissue filling up the intervening spaces, and in place of the thick gelatinous cushion there is the thin gelatinous investment of the cup, already mentioned, in which the blood-vessels ramify. The whole organ, as in *R. batis,* is surrounded by a connective tissue sheath, from which fibres extend inwards to lie between the various rows of cups, and provide for each cup a thin, and often indistinct, fibrous investment.

The lining of the cup (the electric plate) consists of a continuous layer of finely granular protoplasm, containing numerous large nuclei, having a remarkably regular arrangement. Having formed a complete lining for the cup, the electric plate extends over the somewhat sinuous margin to melt and blend with the cortical layer in very much the same way as the electric plate unites with the alveolar layer in *R batis.* The posterior surface of the electric plate lies in close contact with the anterior surface of the striated layer, but it is apparently less easily detached from the striated layer than in *R batis.* For the purposes of description, this electric plate may be described as consisting of two lamellæ—a thick posterior lamella in contact with the striated layer and containing the large nuclei, and a thin anterior lamella which is inseparably connected with the terminations of the electric nerves. The anterior lamella is sometimes separated at irregular intervals from the posterior lamella, owing, apparently, to tension [illegible] of shrinkage of the nerve layer. The nuclei of the electric plate are usually [illegible] sometimes they are nearly spherical. Each, surrounded by a layer of difficultly stainable protoplasm, contains numerous small darkly stained points, the significance of which has not yet been determined The relative size, position, and abundance of these nuclei may be learned by a reference to fig. 5, *e p*.

The distribution of the nerves to the electric cups is indicated in figs. 4 and 5. The remarkable bouquet of nerve twigs which enters each cup can be readily seen in sections of fresh organs fixed with osmic acid. The larger medullated branches divide dichotomously again and again until a countless number of delicate fibrils are produced, which, as they approach the electric plate, lose their white sheath and are only separated from each other by the gelatinous tissue which assists in holding them in position. Some of the terminal branches, magnified 950 diameters, are represented in fig 5 Each terminal branch retains its gray sheath until it reaches the electric plate, and at the point of bifurcation of even extremely small branches a nucleus is usually present. Only a few of these nuclei, however, are represented in the drawing, and the connective tissue corpuscles, which are often large and prominent, are entirely left out, to prevent crowding.

How the nerves ultimately terminate it is extremely difficult to determine. Various views have been advanced as to the nerve endings in the electric organ of the Torpedo, as well as of the Skate; but, as the nerve endings will be specially described in a paper on the structure of the organ of *R. batis*, I shall, in the meantime, simply call attention to the peculiar nerve loops represented in fig. 5, in contact with the anterior surface of the electric plate. These loops result from what appears to be the terminal bifurcation of the non-medullated nerve fibres; hence, they have usually a vertical, or nearly vertical, position, and are only distinctly visible where the section happens to run parallel with the loops, and are indistinct or invisible when the section is at right angles to the loops. Sometimes the loops have an oblique or nearly horizontal position, and when this is the case they often assume the form of complete rings, and when several of these rings are seen at one part of the section in contact with each other the loops seem to have given rise to a delicate network with small, nearly circular, meshes. I have never seen any indication of the nerve fibres expanding to form terminal swellings, or of their giving rise to a plexus in the substance of the electric plate.

The striated layer, as in *R batis*, may be considered as consisting of altered muscular substance. In some sections it still suggests striated muscular fibres (fig. 4, 2 *s.l*); but in most cases the fibres are extremely contorted, as is indicated in fig. 5 (*s.l.*). This layer has a considerable thickness, and, unlike the corresponding layer in *R. batis*, it retains a few nuclei amongst the lamellæ. In transverse sections a number of clefts or spaces are usually seen at irregular intervals between the fibrillæ. These spaces are greatly exaggerated in frozen sections, in which the striated layer somewhat resembles an irregular network, which might be mistaken for the alveolar layer of *R. batis*. The striated layer is directly continuous with the axis of the stem, which consists of the altered posterior portion of the original muscular fibre. In the fully developed cup, however, the greater part of the stem consists of a nucleated sheath continuous with the cortical layer of the cup

The two layers described agree in all essential characters with the corresponding layers in the discs of *R. batis*, but the third, or cortical. layer of the electric cup differs very decidedly from the alveolar layer of the electric disc. The nature of this layer may be gathered from figs 4 and 5 (*c l*). It consists of a thick layer of protoplasm, containing large nuclei, each surrounded by a halo of clear protoplasm. The anterior portion of this cortical layer has, in some preparations, a granular appearance, while the outer is finely striated, but whether the striations have any special significance I cannot say From the cup proper this layer extends, as already mentioned, on to the stem, which it completely invests, diminishing in thickness as it approaches the apex. This cortical layer doubtless agrees with the alveolar layer of *R. batis*. As in *R. batis*, it probably arises from altered muscle nuclei. In *R. batis* the alveolar layer at first consists of a single layer of nucleated protoplasm, but it soon sends out projections, which eventually give rise to a complex network. In *R. circularis*, on the other hand, alveoli are never developed; at the most a few short blunt processes (figs. 3 and 4, *p.*) are thrown out from the outer surface of the cortex, more especially around the base of the stem. It is, however, conceivable that in some other species the outer, or cortical, layer of the cups may develop long complex processes similar to those of *R. batis*. The gelatinous layer, as already indicated, is comparatively unimportant; it surrounds the cups (*c t.*, fig. 5), and fills up the spaces between the stems; it, in fact, forms a matrix in which the cups are embedded, and in which the blood vessels freely ramify. One of the capillaries is represented in fig. 5 (*c.p.*). The capillaries form an irregular network between and around the cups; but they never appear either to enter the cups with the nerves or penetrate into the substance of the striated layer through the cortex.

In a further communication I hope to give an account of the structure and development of the electric cups of *Raia radiata* and to indicate whether I consider them retrograding or progressive structures.*

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* For the material for the above investigations, I am chiefly indebted to the Fishery Board for Scotland. I am also indebted for specimens of various species of Skate to Professor McIntosh, F.R.S, St Andrews; The Maclaine of Lochbuie; Mr W. L. Calderwood, Mr Thomas Scott, and Mr. P. Jamieson (Members of the Scientific Staff of the Scottish Fishery Board); Mr. Sime, Aberdeen, and Dr. P. J. White, Nat Hist. Dept., Univ. Edin. I have especially to thank Dr. G. C Purvis, Dem. Zool. Univ. Edin., for much valuable assistance rendered during the progress of the work.

EXPLANATION OF PLATE 68.

Fig 1 The entire organ of *Raia circularis*, from a specimen 27 inches (68 cm) in length. The sketch was made from an organ exposed by removing the skin and portions of the caudal muscles It measured 8¼ inches (21 cm) in length, and was 5 mm in breadth at the widest central portion. Note the shallow groove (*g*) on the surface of the posterior two-thirds, along which lay the nerve of the lateral line, and note also that the organ is spindle-shaped. Natural size

Fig. 2 Represents a transverse section from near the centre of the organ of *R. circularis*. Note that the organ lies immediately within the skin, and has the nerve (*n.*) of the lateral line indenting its outer surface.

a The skin with four denticles (*a′*.) embedded in the dorsal portion.
b. The lateral fold of the tail.
c. The electric cups
d. The connective tissue surrounding the organ and extending between the caudal muscles
n. Nerve of the lateral line
m Caudal muscles, cut transversely. About six times natural size.

Fig. 2*a*. Represents a thin longitudinal vertical section of the organ of *R. circularis* It shows the arrangement and various modifications of the electric cups, some of which retain, almost complete, the delicate stems. Note that the cups form nearly regular oblique rows.

Ocular 3, objective 00 Outlined with ZEISS' camera.

Fig. 3. Shows one of the cups of *R. circularis*, cut somewhat obliquely. Note the depth of the cup, the great extent of its nucleated lining (electric plate) (*e.p.*) the irregular margin, with a spout-like projection (*s.*) at one side, the cortical layer (*c.l.*) and its blunt processes (*p.*), the thick striated layer (*s l.*), and the long stem (*st.*).

ZEISS' AA, compensating eyepiece No. 12 Outlined with ZEISS' camera.

Fig. 4. Two electric cups, showing the nerves, a portion of the striated layer, the long stems, &c.

n. The nerves proceeding towards the cups.
c.l. The cortical layer, with (in 1.) short blunt projections (*p.*).
s.l. Part of the striated layer.
st. The stem.

ZEISS' AA, compensating eyepiece No. 8. Corrosive sublimate and spirit preparation.

Fig. 5. Longitudinal vertical section through one of the cups of *R. circularis*, showing the three chief layers, the terminal nerve branches, &c.

e p. Electric plate, with large nuclei at nearly regular intervals.

n. Terminal branches of the electric nerve, forming loops and rings as they reach the electric plate. Only a few of the nuclei of the gray sheath are shown in the sketch, and the gelatinous tissue is not represented.

s.l. Striated layer. Note its great thickness, the irregular arrangement of its fibres, and the presence of nuclei.

c.l. The thick cortical layer, with large nuclei embedded in its substance, each surrounded by a distinct halo of clear protoplasm.

st. The stem, invested by nucleated protoplasm, apparently identical with the cortical layer.

c.t. Gelatinous tissue, investing the cup

c p. Capillary, lying in contact with the gelatinous tissue.

ZEISS' apochromatic 4, compensating eyepiece No. 12. Outlined with ZEISS' camera.

XVI. *On the Electromotive Properties of the Leaf of* Dionæa *in the Excited and Unexcited States*.—Second Paper.

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[Plates 69, 70.]

In the paper which I communicated to the Royal Society in 1881, I presented the results of experiments made at various periods during the preceding five years, and the conclusions which I was then able to found upon them. These conclusions, which are set forth in full in the closing pages of my paper ('Phil. Trans.,' 1882, Part 1, p. 1) may be shortly stated as follows :—If by proper means the electrical relation between opposite points of the upper and under surfaces of the leaf of *Dionæa* is investigated while the leaf is "excited," either by touching one of its sensitive filaments or by passing an induction current through the opposite lobe, it is found that the excitation is followed after a few hundredths of a second by a sudden electrical disturbance of less than half a second duration, in which the under surface becomes negative to the upper; and that this is succeeded towards the end of the first second after the excitation by a change of less intensity, but of longer duration and *opposite sign.*

From the character and relative durations (time relations) of these changes, which together, constitute what may be conveniently termed the "excitatory disturbance" or "response," it was concluded that the first was of the same nature with the "excitatory variation" or "action current" of animal physiology, and must be regarded as the expression of a molecular change similar to that which occurs in nerve, muscle, or the electrical organ under analogous conditions. As regards the second, which was designated the "after effect," it was observed first that it was present only when the leaf was "fresh," that is, had not been excited immediately before, and, secondly, that it was associated with the previous and subsequent electrical state of the two "led off" surfaces in such a way that each excitation appeared to leave behind it what might be described as a lasting remainder of the after effect, that is, a permanent and homonymous difference of potential: in other words, that each excitation tended to make the under surface relatively *more* positive if it were before positive, *less* negative if it were before negative, and that, if the leaf were subjected to repeated excitations, it generally happened that the lasting electrical relation between opposite points of its upper and under surfaces underwent a gradual change, that is, the under surface became more positive the longer the observation was continued. It was further observed that in any leaf a similar modification could be brought about much more rapidly by leading through the explored part a very weak voltaic current in the direction of the after effect, that is, from the upper to the under surface.

These facts clearly indicated that what, in the language of DU BOIS-REYMOND, would be called the leaf current, that is, the lasting difference of potential between the two surfaces, has a physiological relation with the phenomena above referred to as constituting the excitatory disturbance. As regards the nature of that relation, it seemed to be indicated that it was in accordance with what, in animal physiology, is called the "pre-existence theory" of the same physiologist, that is, that the "excitatory variation" (see above) is not to be regarded as the setting up of a new electromotive action (action current of HERMANN), but as the result of a sudden diminution of a previously existing electromotive force (in the language of DU BOIS-REYMOND, a negative variation of the leaf current).

On this question, much light has been thrown since the publication of my last paper by the progress of experimental investigation in animal physiology, and particularly by the investigation of the electromotive properties of the ventricle of the heart of the Frog. It was first demonstrated by DONDERS, that the muscular surface of the ventricle when at rest is equipotential, and that electrical inequalities between different parts only manifest themselves either when one or both parts are in a state of excitation, or, in the absence of this condition, when the two parts are in different states of physiological activity. In 1883, I investigated these phenomena with reference to their time relations, and subsequently succeeded in recording them photographically. With reference to the surface of the ventricle, I was able to show (1) that all the facts are comprised in the statement that relative *positivity* of any point of that surface is the concomitant or sign of the physiological endowment of susceptibility of excitation, and (2) that the effect of excitation or injury is to diminish that condition, the degree of diminution increasing with the degree of pre-existing *positivity;* or, more briefly, that the excitable tissue enjoys the faculty of undergoing a change *towards relative negativity* whenever it is interfered with in such a way as either to excite or injure it. Beyond such a statement as this, which involves no physical theory whatever of the nature of the observed relation, it is not, in my judgment, possible to proceed at present. In so far as the so-called theory of pre-existence can be brought within such a definition, I accept it, in preference to the other way of putting it (the "alteration theory"), according to which, devitalised or injured parts are negative, because they are not alive enough, and excited parts negative, because they are too alive.

In comparing the electromotive properties of the ventricle with those of the leaf we encounter on the threshold a difference which requires to be taken into account before proceeding further. This is the absence of localisation in the ventricle, its presence in the leaf. In the former, the excitatory change may take its start from any point excited, and may be propagated in any direction. In the leaf, the change, even when, as in the "fundamental experiment," the impulse is received from the opposite lobe, probably has its chief seat in the sensitive hairs and in the subjacent tissue in their immediate neighbourhood. In my former paper I gave reasons for concluding that in plant tissues the electromotive surfaces are those of *contact between cells in different states of physiological activity*, that is, that when one of the layers of cells is excited, the other remaining quiescent, this gives rise to a difference of potential between them Irrespectively, therefore, of the sign of this difference, it may be assumed that the primary effect of excitation, that is, the first phase of the excitatory variation as described above, is the expression of a sudden difference of activity between the superficial and deeper cells near the upper surface.

If the law above enunciated, namely, that change from the less active to the more active state is accompanied by an electrical change in the direction of relative negativity, holds good in the plant, as in the animal, we should expect that so long as the leaf retains its state of integrity, the upper surface, being the seat of greatest activity, would be positive to the under, and that the response to excitation would consist in a diminution of its positivity. We should also expect that those more gradual changes which in the plant are manifested by the loss of turgor, and which we may compare with the effects of injury in animal tissues, would have their electrical counterparts in equally gradual changes towards negativity of the affected part. And, inasmuch as by our mechanical experiments we know that the loss of turgor, in common with other physiological changes, is localised in the superficial layer of cells of the upper surface, we should expect that complete freshness of the leaf would be indicated by relative positivity (leaf current ascending), diminished turgor by diminishing positivity or equipotentiality, and complete limpness by relative negativity (leaf current descending); and, further, that in the first condition, the sign of the primary excitatory response being in each state opposed to that of the difference of potential, it would in the first state be descending, but as the cells of the upper surface gradually lost their predominance of activity it would be diminished, and finally become ascending

When I resumed my investigation of the leaf of *Dionæa* in 1885, the fact which served as the starting point was the change in the electrical relation of the upper to the under surface which is produced by leading through it a weak descending voltaic current. The investigation of this change soon led to the discovery that the condition of the leaf which I had called normal, in which the upper surface is negative to the lower, is not that of its prime, but one of transition towards a state of diminished activity. Then it was learned that, although the excitatory electrical effects which I had described as belonging to this state are of greater intensity than those which are witnessed when the leaf is in its prime, their right to be called normal is equally questionable; in short, that in vigorous leaves which have been successfully prepared, the state which was before called normal is preceded by a primary state in which the "leaf current" is descending, the excitatory response ascending. My excuse for making this error in 1882 is that the primary state passes rapidly into the secondary, and that the phenomena of the latter, being of greater intensity and more permanent, are much easier to observe. I have only to add that in my new investigations I have had occasion to repeat all my former experiments; and that, although I have learned to understand them better, I have no corrections to make in my experimental results. What was stated was the truth, but not the whole truth.

Section 1.—*Preliminary Study of the Influence of Voltaic Currents led through the Leaf from the Upper to the Under Surface, or in the opposite direction. Discovery of the Process of "Modification."*

Method.—As the phenomena which it was my purpose to observe in the leaf of *Dionæa* correspond as regards their mode of origin to the localised "secondary electromotive" effects which have been during the last few years described and investigated in muscle and nerve by DU BOIS-REYMOND, HERING, and HERMANN.* I had recourse to methods similar to those employed by these physiologists. My object was to lead a current, of which the electromotive force was known, through the lamina for a measured short period (designated the period of closure of the external current), and then, after a certain interval (corresponding to the "Uebertragungszeit" of DU BOIS-REYMOND's experiments), to close the galvanometer circuit through the same electrodes. The arrangements by which this was accomplished were as follows:—

As in the experiments of 1881, the "leading off" or galvanometer electrodes were applied to opposite points on the upper and under surfaces of the lamina, and the difference of potential compensated. Professor DU BOIS-REYMOND's round compensator was used instead of my own.

By a second circuit the leading off electrodes were connected with the poles of a Daniell battery of one or more cells, but in such a way that the current was led through the leaf for a very brief period, which preceded the first closure of the galvanometer circuit and was separated from it by an interval of one-seventh of a second. This was effected by a rheotome specially designed for experiments on secondary electromotive phenomena in muscle and nerve, the construction of which will be readily understood from Diagram 1.

The central circular space p, represents a pulley by which the horizontal bar r r' is made to revolve, say three times per minute. The bar is of sealing-wax, with a core of brass rod. At p, p' and p'', p''' there are platinum wires which pass vertically downwards to such distance as to dip into the pools of mercury ϵ, ϵ', o, o'. a is a fixed trough of brass, which is filled with solid paraffin. Around this a similar trough of the same material, *b*, also filled with paraffin, revolves, so that it can be placed in any desired position with reference to *a*, *c*, is another trough of the same construction as *b*; a short trough, *d*, which travels in an annular groove, so that it can be placed in any required relation to *c*, contains the pool o'; o, o' and ϵ, ϵ' are severally connected with binding screws correspondingly marked out but not shown in the diagram, of which o, o' are in the battery circuit, and ϵ, ϵ' in the circuit of the galvanometer. It will be readily seen that when the bar revolves in the direction of the arrow, o, o' will be first closed, then ϵ, ϵ'; but, inasmuch as the battery and galvanometer circuits are never closed at the same time, and both include the electrodes which are applied to the opposite sides of the leaf, the battery current is led into the leaf during the parts of the revolution limited by the radial dotted lines ω, ω', and the leaf difference led off through the galvanometer during the part limited by the lines η, η'. Before each experiment the instrument is adjusted, and the duration of the contacts, as well as the interval between them, is measured by connecting both contacts with a DESPREZ's time-marker, which inscribes them on a smoked surface.

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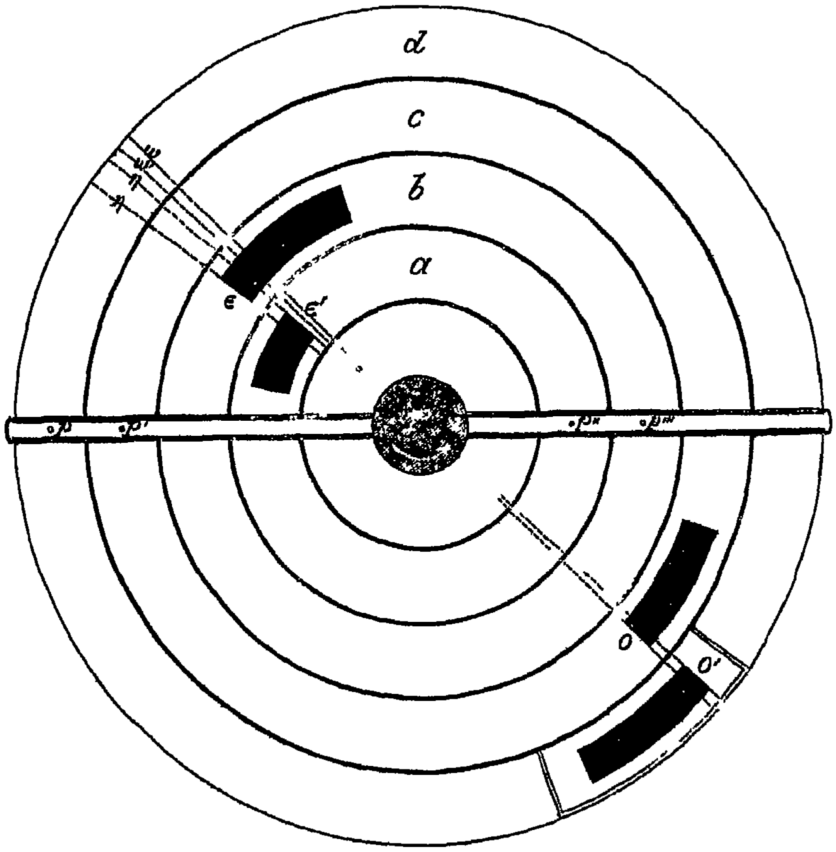
* Translations of the most important papers relating to this subject will be found in the first volume of the 'Oxford Biological Memoirs,' Part 2, pp. 163–380.

Diagram 1



The purpose of this arrangement is to determine not only the immediate effect produced on the leaf by leading through a battery current for a very short period, but also to ascertain the duration and time relations of the effect by measurements made at periods following each other at regular intervals. The method of observation is as follows:—

The revolving bar of the rheotome is placed in such a position that the galvanometer circuit is permanently closed. The difference of potential between the upper an under surface is then compensated, and the bar allowed to revolve. The completeness of the compensation is indicated by the absence of any effect when the wires p'', p''' enter and leave the pools. The battery circuit, which up to this time has been broken, is now momentarily closed by the hand in such a way as to allow the battery current to pass through the electrodes and the leaf *once* during the period ω, ω'. The immediately following effect, and the successive effects which occur at each revolution of the bar (that is, at intervals of 20 seconds) are observed and noted. As the falling time of the galvanometer used is considerably less than 20 seconds, this could be accurately done, so that a series of readings is obtained which, excepting in so far as they may be affected by change of resistance, truly represents the electrical state of the leaf during the period of observation.

The first experiment (July 3) gave the following results :—

The cross difference, i e., the difference of potential between the two opposite surfaces (which in this, as in my former paper, I propose to indicate by the mode of printing the word) was such that the under surface was positive to the upper. Its direction as regards the leaf was consequently descending ↓. It was balanced by 90 divisions of compensator wire, the battery used being a Raoult, that is, a Daniell with half-saturated zinc sulphate solution instead of dilute acid.[*] A battery current of two Daniells was led in in the direction of the difference for four-tenths of a second. The succeeding closure of the galvanometer circuit was of the same duration, *i.e.*, four-tenths of a second, and the interval between the two closures was 0″·14. The successive effects (with one-tenth of the current led through the galvanometer) were very large, the needle being deflected beyond the scale each time; and it was not until a minute after the passing of the external current that the difference became small enough to be measured Half-an-hour later the difference, which was increased as the result of the first experiment, had subsided to ↓80 divisions of wire, and the results with the rheotome (deflections) were (all other conditions being the same) ↓400, ↓70, ↓28, ↓10, and still later ↓100, ↓20, 0, showing that the relative positivity of the under surface is much increased by sending a current in the direction of the difference.

On repeating the experiment on the following day the difference had increased to ↓197 divs.,[†] and the series of deflections observed at intervals of 20 seconds were ↓∞,[‡] ↓∞, ↓∞, ↓600, ↓500, ↓450, ↓370, ↓320, ↓290, ↓270, ↓240, ↓220, ↓180, ↓170. The difference having, as the effect of the passage of the current, increased to ↓280 divs, the current of one Daniell was five minutes later led through in the opposite direction, viz., ↑. The deflections were ↓120, ↓20, ↓10. Then, on again passing the

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[*] With one Raoult element in circuit the value of the whole length of the wire of the "round compensator" is about 0·037 volt. 100 divisions means, therefore, 0·00037 volt.

[†] Here "divs." stands for "divisions of the compensator wire."

[‡] Here the sign ∞ is used, in accordance with custom, to signify that the deflection extended beyond the scale of the galvanometer.

↓ current (the difference having in the meantime sunk to ↓185) we had ↓∞, ↓∞, ↓400, ↓275, ↓210, ↓180, ↓170, ↓160, ↓155, ↓145, ↓120, ↓120, &c., at ⅓′ intervals. Finally, repeating with the ↑ current, as before, the deflections were ↓120, ↓25, ↓18, ↓15, &c. This experiment showed that, although the effect of the ↓ current was about twenty times as great as that of the ↑, both acted similarly.

In confirmation of this, it was found that when the current of two Daniells was led through in the ↑ direction, the deflections were ↓∞, ↓240, ↓130, ↓90, ↓70, &c Subsequent observations of the same kind with still stronger currents showed that, *e.g*, with a ↑ current of six Daniells of the same duration as before, the difference having gradually increased to ↓640 divs, the deflections at 20″ intervals were ↓∞, ↓∞, ↓∞, ↓350, ↓300, ↓260, ↓240, ↓205, ↓190, ↓170, ↓67, &c A few minutes before, a current of one Daniell in the favourable direction (↓) had given ↓∞, ↓∞, ↓420, ↓340, ↓310, ↓280, ↓260, &c, a series entirely comparable with the second of the two examples given above, so that the after effect of the current of one cell descending appeared to be scarcely less than that of six cells ascending.

It was thus evident that the effect of repeated "galvanisation" of the leaf for very short periods is to increase the difference. It was suspected that the resistance of the preparation was diminished, but no measurement was made.

The next step in the investigation seemed to be to ascertain whether the effect of an external current had any relation to the excitatory disturbance, a question which could be answered by determining whether it is associated with any change which is propagated from the part directly acted on to distant parts, and whether it identifies itself as regards the time of its occurrence with the positive (↓) after effect of excitation described in my previous paper. This, it was found, could be decided without any difficulty, as follows:—

The arrangement (July 15) was the same, excepting that, instead of leading through the whole current of one or more Daniells, I used a derivation current led off from a rheochord of which the end-blocks were connected by thick wires with the terminals of the cell, the rheochord wire being divided into 100 equal parts The object was, of course, to increase the external current gradually from a strength at which it was inadequate to produce any effect, to exciting strength, *i.e*, to such a strength as would be sufficient to produce a true excitatory response—one which was propagated to the opposite lobe It was found that when currents of gradually increasing potential were led through the lobe, beginning with 75 divisions and increasing the length of wire by one division after each observation, the transmission to the opposite lobe took place for the first time at 88 divisions, and that until that happened the electrical state of the lobe remained perfectly unaltered. On then observing the condition of the lobe through which the external current was led, with the aid of the slow rheotome, by the method described in the preceding paragraph, we had, after passing a current of a strength just over that necessary to give rise to a propagated effect at 20″ intervals,* deflections of ↓225, ↓15, ↓5; but when the current was increased by substituting two Daniells in series for one, the effect was biphasic, consisting of a ↓ swing followed by a ↑ one off the scale. Comparing these two with the transmitted effects observed under the same conditions when the opposite lobe was connected with the galvanometer, it was seen that, although the ↑ *local* effect of the stronger current was many times as strong, there was no sensible difference in the propagated excitation, which in both cases was characteristic. The conclusion to be derived from this observation is, it need scarcely be said, that the greater part of the local effect is not transmissible, or, putting it otherwise, that it is the sum of two effects, one of which is transmissible, the other limited to the part of the lamina through which the current has passed, and that of the two the latter is much the longest.

In the experiments with the stronger current the existence of an excitatory change was indicated by a preliminary ↑ jerk of the needle; with the weaker current this was not of sufficient duration to overlast the interval.

The observations were now discontinued for a time, in order that arrangements might be made for measuring galvanometrically the strength of the external current used in each experiment. With this view, a second galvanometer was introduced into the battery circuit (July 31). The first observation was a repetition of the comparison made on July 15 of the local with the propagated effect. The results confirmed those previously obtained; they are given below:—

EXPERIMENT I.—Propagated Effect.

Observation.	Direction of external current.	Strength of external current	Effect as led off from opposite lobe.	Difference in divisions of DU BOIS-REYMOND'S round compensator.
1	↓	120	↑250, ↓200, ↓50, &c.	↓100
2	↑	100	None	↓140
3	↓	120	↑310, ↓130, ↓30, ↓30	↓165

EXPERIMENT II.—Local Effect.

Observation	Direction of external current	Strength of external current.	Effect as led off from the lobe through which the current has just passed.	Difference
4	↑	140	↓50, ↓5	↓300
5	↓	150	↑220, ↓∞, ↓100, &c	↓290
6	↓	145	↑440, ↓∞, ↓100, &c.	↓300

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* The reader is requested to notice that, as here, so in the following paragraphs, the series of numbers with ↑ or ↓ signs before them represent deflections observed at 20 seconds intervals.

These two experiments show, as before, that the local after effect much exceeds the transmitted one; that even strong currents when ↑ fail to excite (see previous paper, p. 42); and, further, that, as will be better seen from other modes of observation, when two excitations of the same kind follow each other, the initial galvanometrical effect is stronger in the second than in the first.

The observations of the next few days were directed to a comparison of the local effects of ↑ and ↓ currents, their purpose being to ascertain to what extent the direction is influential. The method was the same, but the period of closure was shortened to one-tenth of a second, and the interval to one-twentieth. The same leaf was observed during two days, the right lobe on August 4, the left on August 5.

In the right lobe the difference was at first ↑500 divs, and in an hour it sank to 370. At this time the current of one Daniell gave when descending ↓∞, ↓110, ↓80, ↓65, when ascending ↑300, ↑220, ↑130, ↑100. The galvanometer in the battery circuit showed the current strength to be the same in the two cases, and it was further found that, whereas the effect of the ↓ current was to diminish the difference, that of the ↑ was to increase it. But on increasing the strength of the external current, by substituting two Daniells for one Daniell, the opposite effects were produced The experiment when repeated in a slightly different way, namely, by leading off derived currents of which the strengths were regulated by a rheochord, gave corresponding results, viz., that up to a certain strength (*e.g.*, 75 lengths of the rheochord wire) the effect was exclusively ↑, that is, in the same direction as the current which caused it; but immediately above this it changed its sign (3.45 p m.), being ↑5, ↓25, ↓25, ↓25, &c , and, subsequently, with a current strength of 150 scale of the control galvanometer, ↓105, ↓40, ↓30, ↓10; still later (4.9 p.m.) with 190 scale, the deflections were ↓220, ↓95, ↓55, ↓35. And it was specially observed that *pari passu* with the change in the immediate after effect, the difference, which was ↑80 divs. at 3.45 p m, changed its sign, and was at 4.11 p.m. ↓55. A further increase of the current strength to 380 scale brought the difference to ↓160, and the local effect to ↑20, ↓∞, ↓∞, ↓370, ↓350, ↓270. In all of these observations one-tenth only of the current was led through the galvanometer.

On the following day (August 5) a similar series of observations were made on the opposite lobe, of which the difference was at first from ↑285 to ↑300 divs At 12.52, with a current strength ascending of 89 scale, we had ↑180, ↑105, ↑100, ↑90; with 150 scale ↑45, ↑35, ↑35; with 180 scale ↓53, ↓35, ↓25; and at 1.10 p m., with 260 scale ↓180, ↓160, ↓100, &c.; then finally, at 1.33 p.m., with 520 scale ↑40, ↓∞, ↓250, ↓230, &c. In this case, as before, the change of sign of the local after effect preceded the change of sign of the difference, the upper surface remaining positive until 1.20 p.m., whereas the after effect became ↓ instead of ↑ at 1.1 p.m. During the course of the experiment, and for some time before and after it, the observations were made regularly every three minutes.

This subject was further investigated (August 6), with, however, this difference, that intercurrently with the observations on the local effect in the right lobe, others were made on the propagated one in the left. As regards the local effect, the results confirmed those of the preceding day. At 12.54 p m. we had, with an ascending current strength of 90 scale through the right lobe, ↓10, ↑30, ↑∞, ↑∞ ; 80 scale gave at 1 20 ↓175, ↓65, ↓50, &c., the difference being still ↑. At 3.22 p m , with a current strength of 240 scale, it was ↑ jerk ↓∞, ↓190, ↓140 At 3.41 p m., with 310 scale, ↑30, ↓ ∞, ↓220, ↓140, ↓100, ↓80 Between the two last-mentioned periods the difference had changed sign being ↑55 divs. at 3 22 p.m., but ↓110 divs at 3.41 p m. In this case the change of sign in the difference was about two hours later than that of the after effect, but during the whole of this period it was diminishing. In this experiment, as in the preceding one, the observations were made at 3 minutes intervals. In each case there was a propagated excitation. Later on the same day we made a similar set of experiments on the right lobe. They were of interest as showing a remarkable point of difference between the local effects of ascending and descending currents.

The observations were begun at 4.20 p.m. A series of current strengths from 2 scale to 26 scale gave no effect. Above this a small ↑ effect appeared, which increased with the current strength, until at 4.50 p.m. we had, with 52 scale, ↑230, ↑260, ↑210, ↑190, ↑130, ↑105, ↑80, and later ↓ deflections, the difference having diminished from ↑ 155 to zero.

During the next 40 minutes the current strength was gradually increased from 65 scale to 380 scale, with the effect of changing the sign, first of the difference, then of the after effect. I give the last five observations tabularly.

Time of observation.	Difference	Current strength.	Local galvanometer effect with rheotome.
P M 5 12	↑5	↓90	↑160, ↑220, ↑190, &c.
5.18	↓20	↓130	↑200, ↑250, ↑230, &c.
5 23	↓60	↓180	↑50, ↑160, ↑100, &c.
5.28	↓140	↓260	↑40 followed by ↓50, ↑25, 0
5 35	↓180	↓380	↑55 followed by ↓190, ↓170, ↓140

The next experiments were made for the purpose of determining more precisely the effects of ascending currents of different strengths It had already been ascertained that a very weak current of the duration of four-tenths of a second produces no after-effect whatever in the same direction, but is followed by a small after effect in the opposite direction resembling the ordinary physical polarisation of PELTIER, and that as soon as the difference of potential at the leading in contacts amounted to something like 0·4 volt the descending effect became much stronger, the actual results being as follows.—

Length of rheochord wire in inches (one inch = 0 006 volt)	Local galvanometer effect with slow rheotome
40	↓30, 0, 0, &c
50	↑8, ↓50, ↓20, &c.
60	↓450, ↓70, ↓30, &c

On August 7 a number of experiments were made with a shorter closing time and interval than had before been used, each being 0″ 07. The leaf was in a perfect state, and its difference was very high (↑918 divs). The external current was derived, as before, from a rheochord wire divided into 100 divisions, of which the difference of potential at the ends was about 0 6 volt. The current strengths were measured by a galvanometer introduced into the derived circuit. The relation between the length of wire and the current strength depended, of course, on the resistance of the preparation, which, as will be shown later, tends to diminish, but in the present instance was fairly constant. With very feeble ↓ currents it was observed that the effect of the first closure was to render the upper surface of the leaf more positive, the difference gradually increasing from ↑400 to ↑918. A second closure of which the current strength was 9 divs. gave a very small ↓ deflection, preceded by an ↑ jerk, then ↓22, ↓26. Subsequently a current strength of 18 scale gave ↓∞, ↓50, ↓30, ↓10 ; 35 scale gave ↓∞, ↓190, ↓50, &c. Up to this point it was ascertained by leading off from the lobe to the galvanometer *that there was no propagated effect* The strength of the external current was then increased to 78 scale, which gave ↓380, ↓200, ↓150, &c., and it was found that each excitation was followed by a permanent diminution of the difference, and that an excitatory effect was propagated to the opposite lobe.

An hour-and-a-half had now passed, during which the external current had been led through the leaf 25 times, that is, for an aggregate duration of a second-and-three-quarters. Its upper surface was still positive, but its positivity was evidently diminishing. At 5.30 p.m. the difference was still ↑147, at 5.52 p m. it was ↑95, at 6.12 p m. ↑50, at 6 43 p m. ↓125. In all, eight currents had been previously sent through it of above exciting strength, but during the period between 5.30 and 6 50 p.m the lobe remained untouched. It thus appears that the gradual change of modification in the electromotive relations to each other of the upper and under surfaces of the laminæ, when once started by external currents, continues without external interference.

Section 2.—*Further Study of the Process of " Modification."*

By the observations related in the previous paragraph, it had been learned that the effect of leading weak currents through the leaf of *Dionæa,* especially if they enter by the under surface, is to produce a permanent and progressive change in its electrical condition. I have now to add some observations made for the purpose of studying the nature of this modification.

On August 12 experiments were made in which a leaf, of which the left lobe was connected with the galvanometer, was excited mechanically on the right side, as in the fundamental experiment, by touching the hairs with a camel-hair pencil. The excitations occurred at intervals of three minutes during half-an-hour. The difference was descending, and remained so. It was balanced by from 130 to 141 divs., and produced when one-hundredth of the current was led through the galvanometer a deflection of 25 scale. At the end of the period mentioned, a current of a single Daniell was led through the leaf twenty times at intervals of 20 seconds, the current being each time three-hundredths of a second. The immediate local effect of each external current was led off to the galvanometer during the interval which followed each leading in. There occurred therefore, as before, a series of excursions at 20 seconds intervals, by which the progress of "modification" was indicated. These were (one-hundredth of the current passing through the galvanometer) ↑22, ↑20, ↑18, ↑0 0, ↓15, ↓26, ↓35, ↓40, ↓52, ↓57, ↓67, ↓71, ↓75, ↓76, ↓80, ↓85. On connecting the surfaces of contact with the galvanometer without the rheotome, there was a deflection of ↓200 scale, which was balanced by 320 divs., but rapidly subsided to ↓150.

The leaf having been thus completely modified, it was subjected to a second series of mechanical excitations as before, lasting for an hour. The rough galvanometric results of these excitations are compared below with those before modification.

Before	3 20 to 3 50 p m.	↑20 ↓270	↑25 ↓225	↑20 ↓220	↑15 ↓225	↑20 ↓260
After	4 20 to 4 50 p.m	↑400 ↓300	↑370 ↓400	↑350 ↓400	↑260 ∞	↑330 ↓700

The difference had diminished from ↓200 to ↑25.

At five o'clock the external current was again led through the same way as before, but only ten times instead of twenty. Each passage of the current was followed by an increase of the relative negativity of the upper surface of the leaf, the effect of which showed itself, when the galvanometer circuit was closed at the end of the period during which the leaf was acted upon, by a difference corresponding to 500 divs., which declined as before, so that three minutes later it was balanced by 380 millims. Taking the mean of five galvanometrical observations, the effects of excitation at intervals of three minutes now gave (with one-tenth of the current through the galvanometer) ↑105·0 ↓14 5; so that we have, as the general result, the excitatory effects observed in successive stages of modification:—

Before	↑2 ↓24
After modification	↑34 ↓45
After further modification . . .	↑105 ↓14

All of these are given in round numbers as they would have been observed had one-tenth of the current been led through the galvanometer.

On August 13 a leaf was prepared and observed, as in the fundamental experiment, with leading off contacts on the left lobe. The difference was compensated by 920 divisions of wire, and gave (with one-hundredth of the current through the galvanometer) a deflection of ↑330 scale. The transmitted effect of mechanical excitation of the right lobe was ↓10 ↑70, and that of electrical was similar (mean of three observations with one-tenth of the current through galvanometer, ↓5 ↑31). Without shunting, it was seen that the ↑ phase was preceded by a jerk of the needle in the opposite direction. After an hour, during which the difference was little altered, the leaf was modified by passing feeble external currents through the leading off electrodes of one-twentieth of a second duration at 20″ intervals, but no further observations were made till next morning.

At 11.30 next day the difference was found to have changed sign (↓48 divs.). During the next hour-and-a-half the transmitted effects of the electrical excitation of the opposite lobe were observed. The difference gradually increased from 48 divs. to 120 divs. In order to obtain a notion of the character of the transmitted effect, curves were sketched after each observation, which, however, are valueless as records, as not truly representing the time relations of the electrical changes which produced them; for, as will be seen afterwards, the excitatory effect lasts little more than a second, whereas the swing of the needle to which it gives rise lasts the greater part of a minute. The final effect of each excitation was to increase the difference, so that the length of wire required for compensation increased after each excitation, the numbers (divs. of compensator) being 48, 48, 50, 65, 75, 83, 95, 102, 108, 120. On now leading weaker ascending currents through the electrodes of one-twentieth of a second duration ten times at 20″ intervals, and closing the galvanometer for the same time after each excitation, we had, as the immediate local result of each current, ↑15, ↑15, ↑10, ↑5, ↓3, ↓15, ↓22, ↓25, ↓28, ↓33, and at the end of the process, instead of 120, 600 divs. of wire were required to compensate the difference. The excitatory effect had undergone a corresponding change, giving now as large deflections when one-tenth of the current passed through the galvanometer as it had previously done with the whole.

On the following day (Aug. 14) a similar observation was made, of which the results were still more striking The leaf was prepared at 3 P.M. The lobe, of which the surface was connected with the galvanometer, showed at that time an ascending difference which was balanced by 480 divisions of compensator wire, subsequently by 550, 576, 560 divs. The transmitted excitation effect was ↑3, ↓48 as observed with one-tenth of the current through the galvanometer, but when it was observed without shunting it could be seen that the ↓ effect was preceded by a jerk of the opposite sign. At 3.35 P.M. a ↓ external current was led through the leaf of 0″·03 duration, and repeated at intervals of 20″, as before, for five times. Each was followed by a change in the condition of the leaf, the immediate after effect being ↓10, ↓25, ↓53, ↓65, ↓105; and at the end the difference, which just before had been ↑487, was found to have altered its sign, being at first ↓815, then gradually increasing to about 900 (these numbers, of course, indicating the length of wire required for compensation). The excitatory effect was represented by ↑265, ↓183·3, these numbers being the means of six successive observations made between 3.45 P.M. and 4 P.M., one-tenth of the current passing through the galvanometer. Once more the same process was repeated, that is, a current of the same strength was led through at 20″ intervals, with the effect of bringing up the difference to 975 divs, the mean of six observations being ↓308 ↑50. Thus, we have the following striking contrast:—

	Difference	Excitatory effect.
3 30 P M—Before modification .	↑576	↑3 ↓48
3.45 P M—After modification	↓900	↓265 ↑183
4.0 P M—After further modification .	↓975	↓308 ↑50

This observation made it clear that the condition of the leaf which in 1881 I had regarded as normal, is preceded in vigorous leaves by another in which the galvanometrical effects are much smaller, the "leaf current" is in the opposite direction, that is, ascending, and the first phase of the excitatory effect descending. It was also apparent that the small galvanometric effect of the variation in the unmodified state was in part due to the very high resistance which then prevailed; for, whereas after modification one hundred divisions of compensator wire gave a current of 280 scale, the same length of wire before modification gave only 123.

Section 3.—*Observations as to the influence of conditions other than the passage of External Currents in producing "Modification." Proof that the Effect of the Current does not depend on its evoking an Excitatory Response.*

The first of these series is important, as showing that, although "modification" is immediately and with certainty effected by the passage of an external current, the antecedent state may last for some time even when the leaf is repeatedly excited, and (as had often been observed before) that the two lobes may be in very different stages, notwithstanding the complete identity of the conditions under which they have been placed.

The contacts were arranged for leading off from either lobe as required. The right lobe showed the antecedent state, the other was in a transitional one—the difference being on the right side ↑1050 millims.,* on the left ↑29 During a period of 40 minutes the leaf was excited mechanically at intervals of 3 minutes, each lobe receiving six excitations, of which the first five were led off from the opposite lobe, and those of the last of each series from the same lobe.

The characters of the five propagated effects were as follows —On the right side (small difference) the first phase was negative from the first, and gradually increased from 6 to 30 scale (with one-tenth of the current), and was followed by a deflection of more than four times the extent in the opposite direction. On the left side, when the whole current was allowed to pass through the galvanometer, the same phenomenon as before described was witnessed, namely, that the swing of the needle in the ↑ direction was at once caught by a movement to the opposite side, and this was followed by a ↑ swing of much greater extent (over 400 scale)

The two observations in which the effect was led off from the excited lobe showed substantially the same phenomena (with one-tenth of the current).

Right lobe	↑jerk, ↓jerk, ↑48.
Left lobe . . .	↑35, ↓150.

A ↑ current of 4 Daniells was now passed for three-twentieths of a second through the left lobe, and four times repeated at intervals of 20 seconds. It was found that the right (opposite) lobe was unaltered, that is, still remained in the antecedent state (diff., ↑920; exc. effect, ↓18 ↑73). In the left lobe the difference had changed sign, being now ↓1100, instead of ↑340, and the excitatory effect (with one-tenth of the current through the galvanometer), ↑270 ↓ off the scale, that is, over 300; this observation having been confirmed by repetition, five ↑ currents of the same strength and duration as before were led through the right lobe. Immediately after the difference had changed sign, and was now ↓858 instead of ↑920, and the excitatory effect, ↑230 ↓270. In other words, the two lobes, which were in the first instance in such different stages of modification, were when subjected to the same modifying process brought into perfect conformity with each other.

The preceding experiment shows that the influence of mechanical excitation in producing modification cannot be compared with that of a current, for both lobes were repeatedly excited mechanically without any material change in their electrical state, and it was further observed that the modification of one lobe had no effect on the other, as would have been the case had the result been producible by propagated excitations. It could, therefore, scarcely be supposed that the modifying influence of the current is at all dependent on its evoking an excitatory reaction; but to make this clear it appeared desirable to repeat the preceding experiment, taking especial care that the currents used should be below exciting strength.

On October 5 a leaf was prepared with leading off contacts on the right lobe.

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* In these experiments a compensator, of which the wire is divided into 1200 millims, was used 100 millims. of wire corresponded to about 0·0074 volt

The difference was ↑810, and the excitatory effect of mechanical excitation of the opposite lobe was (with one-tenth current) ↓10, ↑20. With the whole current through the galvanometer, it was seen that the initial ↓ phase was preceded by a ↑ jerk of the needle. Five series of very feeble ↑ currents, each of 0″·22 duration, were passed through the lobe by means of the slow rheotome, which, as in the previous observations, was so arranged as to close the leading off circuit for a period of half a second after each excitation, so as to afford an indication of whatever change might occur in the electrical state of the surfaces led off from. There were in all 40 closures. Up to 20 closures the deflections were still ↑, but between 20 and 30 they gradually became ↓, increasing at the same time in amplitude. The after effects had therefore changed sign, but even after 40 closures the difference was found to be still ↑. The leaf was then subjected during the next quarter-of-an-hour to a series of excitations at one minute intervals, in the course of which the difference, which was at first balanced by 240 divs., gradually diminished to 0, and then changed sign, so that at the end of the observation it was ↓40. The second phase of the excitatory effect gradually diminished in extent until it disappeared (at first ↑50 ↓105, eventually ↑65 ↓0). The leaf was left in the moist chamber until the next day (19 hours). Its upper surface was now strongly negative, the difference being ↓510, and the excitatory variation (with one-tenth current) ↑70 ↓280. These results confirm the evidence previously given, that the process of modification once started in the leaf is a progressive one, for the change which was observed immediately after the passage of the current not only went on rapidly during the next half-hour, in the course of which it was excited mechanically, but continued during the night, notwithstanding that the leaf was not interfered with.

Our next endeavour was to ascertain whether, by methods other than electrical, it was possible to initiate a similar series of changes. For, inasmuch as it so often happens that leaves which have certainly not been subjected to the action of any external current exhibit the condition which in others results from modification, it seems clear that the current acts merely as a stimulus by which a physiological process, for which the essential conditions are internal, is called into activity. With this view, various observations were made during the first week of October, 1885, on leaves of which the under surface was negative to the upper, and the initial phase of the excitatory disturbance was ↓, for the purpose of ascertaining whether, either by mechanical excitation or by the application of heat to the surface (by bringing near it a small platinum coil through which a current was flowing), the process which has been described could be initiated. It was found that in some leaves the change began as soon as the leaf was prepared, that is, that when first observed it was in a state of change, which was sometimes so rapid that the length of wire required to balance it was reduced to a half or a third in a few minutes. In such leaves it was always found that the change was promoted either by warming or by touching the sensitive filaments of the opposite lobe, but we were not able to find that either of these expedients produced effects comparable to that of leading through an external current.

Section 4.—*Observations relating to the Influence of "Modification" on the Electrical Resistance of the Lamina.*

In the course of the preceding observations it had been learned that, in general, the extent of the galvanometric effects was much larger in the modified than in the antecedent state; and it was surmised that this was partly due to diminished resistance. To determine this, a simple but sufficient method was adopted—that of passing through the leaf by the electrodes used ordinarily for leading off, before and after modification, a current derived from the same length of compensator wire. The ratio of the two galvanometer readings thus obtained, for a reason to be immediately referred to, affords a sufficiently exact indication of the difference of resistance. Thus, in a leaf examined on October 2 it was found that 100 divs. gave through the right lobe, which had not been modified, a deflection of 38 scale, through the left, partly modified, 150 scale; but after both had been completely modified by the passage of a current through them, the same length of wire gave a deflection of 360 in the right and of 340 in the other. It was thus evident that in the modified state both were, as regards resistance, in the same condition. In another leaf, which was the subject of observation on October 9, the same difference of potential which gave a current of 38 scale before modification gave 110 when it had just changed sign, that is, immediately after passing the modifying current.

To elucidate the effect, the following more exact, but more circuitous, method was adopted —

Two Daniell cells were connected with the end-blocks of the compensator, in the circuit of which a variable resistance was interposed, so that the difference of potential between its ends could, within certain limits, be varied at will. One of the end-blocks was connected through a fixed resistance (30,000 ohms) to the shunt of a galvanometer, the wire from the other terminal being led to the slider of the compensator. The resistance in the compensator circuit was then adjusted so that 100 millims of wire gave a deflection of 300 scale in either direction.

This having been done, the leading off electrodes were applied to the opposite surfaces of the leaf, and the leaf, with its electrodes, so introduced into the galvanometer circuit as to take the place of the fixed resistance. The ↑ difference was balanced by 210 millims. of wire (the value of which in actual difference of potential was now about twice as great as in the previous experiments), and 10 millims. gave through the leaf a deflection of 355 scale (one-tenth of the current). The propagated effect was (mean of five successive observations) when observed with the whole current through the galvanometer ↓29, and was preceded by a small preliminary jerk of the needle in the ↑ direction, followed by ↑ after effect. The lobe was therefore completely unmodified. The current of two Daniells was now led through in the ↓ direction for 30 seconds. The difference had changed sign, and was now ↓640, instead of ↑200, the first phase of the propagated excitatory effect being ↑160, instead of ↓3. The resistance had undergone an equally remarkable change, for the same difference of potential, which a few minutes before gave a deflection of 35·5 scale, now gave (mean of seven observations) 335 scale.

As the resistance of the galvanometer and electrodes together was about 7000 ohms in both of the experiments on the leaf, whereas in the preliminary experiment the total resistance in the circuit was about 32,000 ohms, we have, designating by R the resistance of the lobe before modification, and by R′ the resistance after modification, the following relation. The difference of potential corresponding to 100 millims. of wire gave, with the resistance 30,000 ohms, a deflection of 300 scale. In the second experiment, with the resistance R in the leaf, in addition to 7000 ohms in the circuit, the same difference gave 35·5 scale. In the third experiment, after modification, with the resistance R′ in the leaf, in addition to 7000 ohms in the circuit, the deflection was 246 scale.

Consequently,

$$R = \frac{300 \times 32{,}000 = 9{,}600{,}000}{35{\cdot}5} - 7000 = 263{,}422 \text{ ohms,}$$

and

$$R' = \frac{300 \times 32{,}000 = 9{,}600{,}000}{246} - 7000 = 32{,}024 \text{ ohms.}$$

In a similar experiment with another leaf, we had with the invariable resistance 330 scale, with the unmodified leaf 155 scale, and after modification 375 scale.

Consequently,

$$R = \frac{330 \times 32{,}000 = 10{,}560{,}000}{155} - 7000 = 61{,}120 \text{ ohms,}$$

$$R' = \frac{330 \times 32{,}000 = 10{,}560{,}000}{375} - 7000 = 21{,}160 \text{ ohms.}$$

Hence, in the first experiment the ratio of the resistance in the modified leaf to that in the unmodified was 1 : 8, in the second 1 : 2·9.

Had we considered the deflections without taking into account the difference of resistance in the circuit, we should have had in the first experiment 1 : 6·95, in the second 1 2·40. The resistance of the leaf is so enormous, as compared with that of the circuit, that for the purpose we have in view the latter may be neglected.

In the other examples given, the ratios were 1 : 9·5, 1 · 2·3, and 1 : 2·8. The great difference between them is readily explained by the circumstance that, although apparently every leaf can be brought into the modified state, the process of modification has in many instances already made some progress before the resistance can be measured.

Section 5.—*Investigation with the aid of the Pendulum Rheotome of the Time Relations of the excitatory Variation in the Modified and Unmodified states of the Leaf.*

I have now to give an account of two series of observations, made respectively in August and October, 1887, which were undertaken for the purpose of confirming and correcting the knowledge which had been gained in 1885, with respect to the nature of the change which, in the preceding section, has been termed "modification." In the first series my object was to determine the time relations of the excitatory process in the unmodified and unmodifiable states respectively, with the aid of the rheotome, in the second to obtain photographic records of the characteristic electrical phenomena.

Observations with the Rheotome.

The pendulum used for the purpose was one which has been recently constructed in the Oxford Laboratory. Its period of oscillation is 1″·4.

The arrangement of its keys is the same as in an instrument I employed in 1881, but for the present purpose it has the advantage that, in consequence of its much greater length, a much longer period can be investigated. The leaves were prepared in the way described in my previous paper, and were placed in a moist chamber at the ordinary temperature of the room in August The temperature varied during the experimental days from 60° to 67° Fahr. Each leaf was, of course, provided with two pairs of non-polarisable electrodes, which were applied, one to the upper surface between the three hairs, the other to the under surface exactly opposite. The direction of the break induction shock produced by the zero key of the rheotome was, of course, always (↓) descending; and in all the experiments the period of closure (the interval of time between the opening of the short circuiting key (K_2) and the opening of K_3) was the same, namely, one-tenth of a second *

The observations were made on Aug. 13, 15, 16, 17, 18, 1887, and are numbered 1, 2, 3, 4, 5. It was found convenient to use as a compensator a German silver wire 300 inches long, divided into 100 equal parts The value in volts of each division was determined subsequently. It was 0·014 volt.

In four of the observations the method was exactly the same. Two series of rheotome observations were made, the first series with the leaf in the condition in which it presented itself when first prepared, the second after it had been modified. The modification was in each case effected by passing the current of two Callaud's cells six times through the leaf for ten seconds each time, reversing the direction each time, so that three currents were descending and three ascending. The diagrams give the result The intervals between successive excitations were about one minute each; sufficient time was thus given to allow of the difference being satisfactorily compensated. The amount of the difference was of course recorded in each case.

In each of the diagrams the dots connected by faint unbroken lines indicate the rheotome observations of the excitatory reaction in the unmodified leaf, made during the first eight-tenths of a second, the numbers being the deflections observed when the time of closure (the duration of which, as above stated, was always 0″·1) ended 0″·1, 0″·2, 0″·3, 0″·4, 0″·5, 0″·6, 0″·7, or 0″·8 after excitation. The dots connected by broken lines relate to observations of the deflections observed when the galvanometer circuit was closed during the whole of the second or third second respectively by the hand guided by the metronome. The dots connected by *stronger* unbroken lines, and the numbers, have the same meaning with reference to the excitatory variation in the modified state

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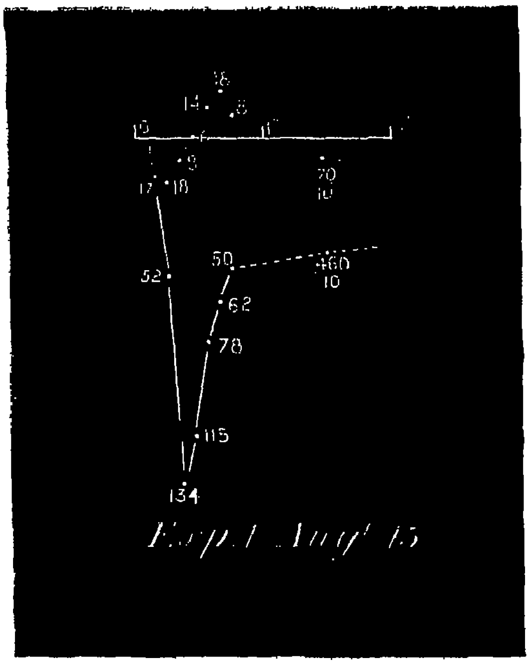
* See 'Phil Trans.,' 1882, p 18, and fig 8

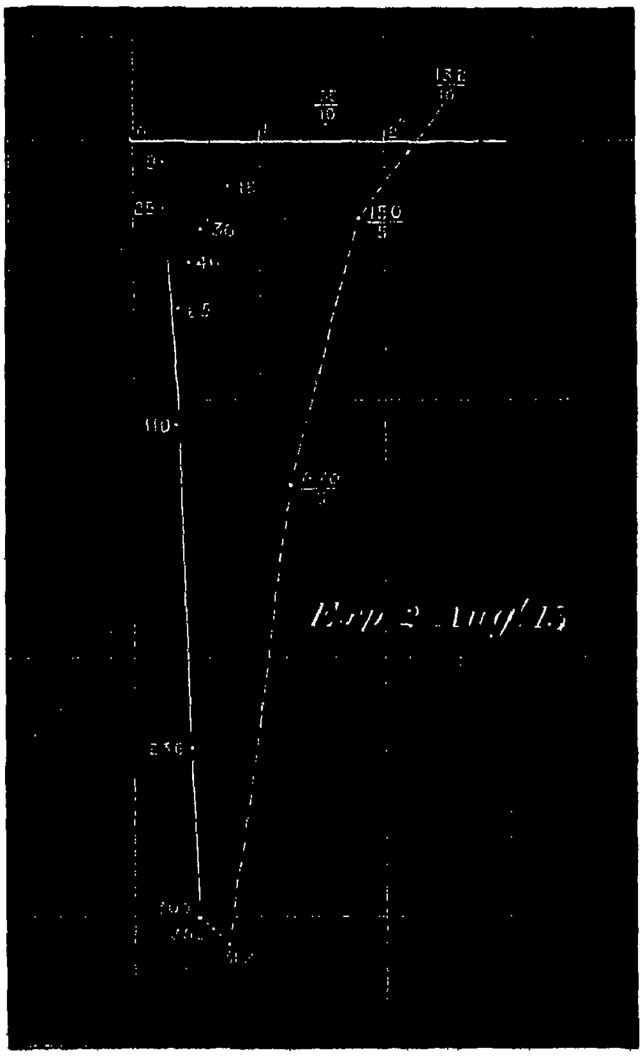
Experiment I. (diagram 2).—In this experiment the difference when the leaf was prepared was high (↑16·3). At the beginning of the rheotome observation it was ↑15, and fell during its course to ↑13. The excitatory effect, as observed with the galvanometer, was ↑10, ↓15, ↑250, that is, it was a long ascending swing preceded by an oscillation. The rheotome showed that the oscillation, though its galvanometric effect occupied several seconds, was over before the end of the first second. Immediately afterwards modification was effected (this time by passing the current of one Callaud ↓ for 20 seconds). The difference was now ↓2·1, and in the excitatory effect no preliminary oscillation was visible, only a negative swing followed by a prolonged after effect in the opposite direction. The resistance was much diminished, so that the same length of wire which gave a deflection of 9·2 before now gave 69.

Diagram 2.



In *Experiment II.* (diagram 3) the difference, which was at first 8·5 wire, increased during the observation to 12·5. As the alternate short currents did not produce the desired effect, the current was closed in the ascending direction for a minute, after which the difference changed sign. It was at first ↓7, but subsided during the rheotome observation to ↑4·5. The diminution of resistance was such that with the same length of wire the deflection representing the difference, which before modification was 370 scale, increased after modification to 115 × 10, that is, 115 scale, with one-tenth of the current through the galvanometer. It will be noticed that in this leaf the resistance both before and after the passage of the external current was much less than in Experiment I. When the first rheotome observation was made, the excitatory variation was (with the galvanometer) ↑120, ↓220. It showed already, therefore, the characters of the "modified state," although the difference was still ↑. But from the rheotome readings it appeared that the first phase was of relatively short duration, for during the second half of the first second the relative negativity of the under surface was very rapidly diminishing, and during the second second it was reversed. The comparison of the two records shows that the change of sign did

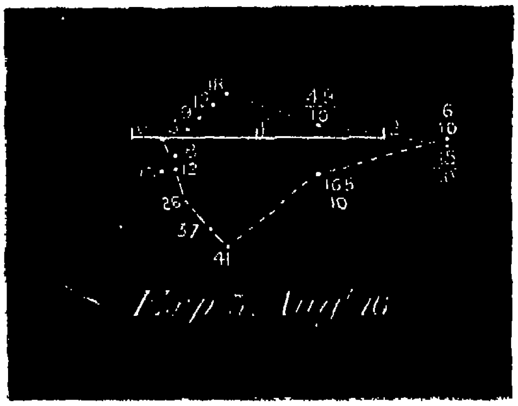
Diagram 3



not occur until a second later, the operation in the less modified state of what may be designated the ↑ element in the excitatory effect of the external current being to annul this action, or so far to diminish it as to give complete predominance to its opposite. Here again it must be noted that the great amplitude of the deflections in the second rheotome observation was due to diminution of resistance.

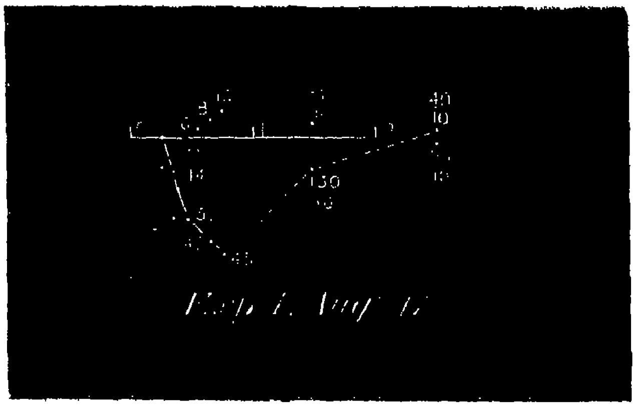
Experiment III. (diagram 4).—In this preparation the difference remained constant, namely, between 14 and 15, during the whole observation. The excitatory effect was observed with the electrometer, and had the character shown in photograph 13 (Plate 70). The rheotome observation showed that the oscillation was, as in Experiment I., completed during the first second. After modification, which was promptly effected in the usual way, the difference changed sign from ↑7 to 0, or ↓0·5, and the prevailing direction of the excitatory effect became ↑; so that in every respect but one, the curves are seen to be counterparts of each other. Both effects began in the same direction, but in the modified preparation the initial negative phase, which before modification is interrupted or cut short by an effect in the opposite direction, rose to its highest point at about the same time after excitation as the positive phase had culminated before In both conditions there was an after effect, but the two after effects had opposite signs. In the unmodified state the under surface became more negative as a consequence of each excitation; after modification it became more positive. The diminution of resistance was as great as in the other cases. With equal lengths of wire the deflection before modification was 160 ; after, 110 × 10.

Diagram 4



Experiment IV., *Aug.* 17 (diagram 5).—In preparation IV. the difference was 61, but, as in Experiments I. and II., diminished considerably before the rheotome observation could be taken. For the purpose of bringing about modification, the current of two Callaud cells was passed through the right lobe for one minute, changing the direction every ten seconds. One such operation failed to produce the desired result, the difference remaining in the old direction; but after a second minute it had changed from ↑2·5 to ↓3·0, and there was a corresponding change in the excitatory variation as observed by the electrometer. Before modification the excitatory effect consisted of an excursion in the ↓ direction, which was preceded by a sharp jerk in the ↑, and followed by a prolonged ↑ after effect. After modification a preliminary ↓ effect was followed by a prolonged ↑ after effect. With the same difference of potential, the galvanometric deflection was 68 after modification, 26 before.

Diagram 5.



Experiment V., *Aug.* 18 (diagram 6).—Here the difference was ↑10 6, but diminished to 9 3 during the first rheotome observation. The character of the excitatory effect resembled that observed in Experiment III., but the ↓ phase lasted longer. The after effect, as in Experiment III., was ↓.

Diagram 6.

A second observation was made an hour after the first, in which the preparation was found to be changing in the direction of modification, though no extraneous current had been led through it, for the ↓ phase was both weaker and of much shorter duration, as evidenced by the fact that during the second second the under surface was feebly negative, instead of strongly positive Modification was promptly effected in the usual way. The difference, which had diminished to ↑5·6, changed sign and became ↓3·5, and the resistance had so diminished that with the same length of wire the deflection, which had before been 280, became 75 × 10. In this case the electrometer displayed the change which had occurred in the electrical response very strikingly. Before modification it resembled photograph 12; after, photograph 1.

Section 6.—*Photographic Records.*

I have now to submit to the reader, in further illustration of the nature of the excitatory effect, as observed before and after modification, a series of photographic records (Plates 69, 70) obtained by a method which I used in observations made some years ago on the Electromotive Changes in the Heart, and published in the 'Journal of Physiology,' vol. 4, p. 327.

This method consists in connecting the leading off contacts of the leaf to the capillary electrometer, instead of the galvanometer, and photographing the movements of the mercurial column. For this purpose the capillary is projected by means of a half-inch objective on a slit at a distance of about two feet. Immediately behind the slit a photographic plate moves horizontally, with a velocity of about 1 centim. per second.* The photographic curve thus obtained expresses the movement of the column during the period of observation, viz., about 25 seconds. In most of the experiments time was marked on the plate photographically by a vibrating shutter, which covered one end of the slit, and was opened by an electro-magnet in circuit with a tuning-fork, either ten times or twenty times a second, producing a dark bar on the plate each time it was opened.

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* This method is here described as used for my observations on *Dionæa.* It has since been considerably improved, and will be described in a future communication

Photographs 1, 2, 3, and 4 represent experiments made in 1883, the mode of observation being precisely that described in my former paper as used in the "fundamental experiment." Photograph 1 may be considered as a typical record of the excitatory variation in a modified leaf when subjected to repeated excitation by passing a weak induction shock through the opposite lobes and in the ↓ direction every five seconds. The four photographs differ chiefly as regards the duration of the primary effect, or ↑ phase (descending in the photograph). In all, it is seen that the first phase begins about one-fifth of a second after the moment at which the current in the primary coil of the induction apparatus is opened (in accordance with the rheotome observations), and that the primary effect of the first excitation is followed by an after effect in the same direction, and that this after effect is neither increased nor diminished by the succeeding excitations, but subsides gradually during the whole period of observation. In photograph 6 it is seen that when the interval between succeeding excitations is longer, so that the after effect has time to subside, the second effect resembles the first, though the second phase is of less amplitude. Photograph 5 is the record given by the same leaf as photograph 2, when "exhausted" by repeated excitation. The difference is greater, and the resistance less; the first excursion of the electrometer exceeds the rest in amplitude, but *is followed by no after effect* (see 'Phil. Trans.,' 1882, Part 1, p. 31). In the observation recorded in photograph 7 the opposite lobe was excited, not electrically, as in all the preceding instances, but mechanically, by touching the tips of the sensitive filaments with a camel-hair pencil, which was so used as at first to touch a single filament and afterwards accidentally two filaments. It is seen that, although in each of the double excitations the interval between the two immediately following effects was about three-quarters of a second, there was little difference between them in amplitude.

Photographs 8 and 9 are records of an experiment in which the leading off contacts were on opposite and corresponding spots on the middle of the under surface of the two lobes, as shown in my former paper ('Phil Trans.,' *loc. cit.*, p. 36, fig. 13). The right lobe was connected with the sulphuric acid, and the left with the mercury, that is, with the capillary. In the first observation the right lobe was excited by touching one of the sensitive filaments with a camel-hair pencil in the neighbourhood of the leading off contact; in the second, the excitations took place alternately on opposite lobes, that is, in the neighbourhood of the two opposite leading off contacts. It is seen that in the first case (photograph 8) the under surface of the right lobe becomes first relatively positive, then that of the left; and in the other that the same diphasic effect is witnessed as the result of the first and third excitations, but that the effect of the second and fourth are counterparts of the others, the explanation being, of course, that in the first and third excitations the right lobe was first excited, in the second and fourth the left, and that in either case the effect showed itself first in the excited lobe, later in the opposite one. Photograph 10 represents an observation in which the sensitive hairs on the left lobe in the neighbourhood of the leading off contact were successively touched, in the same way that those of the right lobe had been in the preceding observation. It is complementary to 8 *

It will be understood that all of the preceding photographic records relate to the unmodifiable state, and that in every instance the upper surface was positive to the under. Figs 11 and 13 (Plate 70) relate to the previous condition. They are records of the excitatory effects in leaves in which the " leaf current " is descending, that is, in which the upper surface is still positive to the lower.

Photograph 11 represents the usual form of such a tracing It is seen that the electrometer effect consists of (1) a momentary ↑ effect, in which the mercury receded for a period not exceeding one-tenth of a second ; (2) a longer excursion in the opposite direction, which lasted about four-tenths of a second, and that the after effect, in which the negativity of the under surface of the leaf was much increased, attained its maximum about a second after excitation, and gradually declined subsequently. It is also seen that, as in the permanent state, the after effect is neither increased nor diminished by the subsequent excitation. At the time the photograph was taken the relative negativity of the under surface (difference) was about 0 11 volt. This was increased to about 0·14 as the after effect of the excitation.

Photograph 12 is introduced to show the reversal which the excitatory effect undergoes in consequence of modification. In both, as has already been shown by the rheotome observations, the first effect is negative, but in every other respect the two tracings are counterparts, the period of negativity in either surface in the one corresponding to that of positivity in the other When the second photograph was taken the relative positivity of the under surface was about 0 005 volt, but subsequently increased to about 0·03 volt.

The large after effect seen in photograph 9 is only observed when the leaf has not before been excited, or has been excited only once or twice. It expresses, therefore, a state of things which is very transitory. A more easily observed condition is that in which there is no after effect, and the variation consists simply of the primary ↓ excursion with its ↑ precursor, as in photograph 13.

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* These tracings may be compared with the photographic records similarly obtained of the diphasic excitatory effect in the ventricle of the heart of the Frog or Tortoise (see 'Journal of Physiology,' *loc cit.*, Plates 1 and 3). The conditions of the observation correspond, and the effects are in harmony with each other

ADDENDUM.

The following experiment was made for the purpose of obtaining experimental proof that, in the process of modification, the change has its seat at or near the upper surface of the lamina, and does not affect the under surface. It was anticipated that if one lobe were modified, leaving the other in its original state, the comparison of the electrical relations between symmetrical points of the upper and under surfaces respectively would afford the required demonstration.

Diagram 7

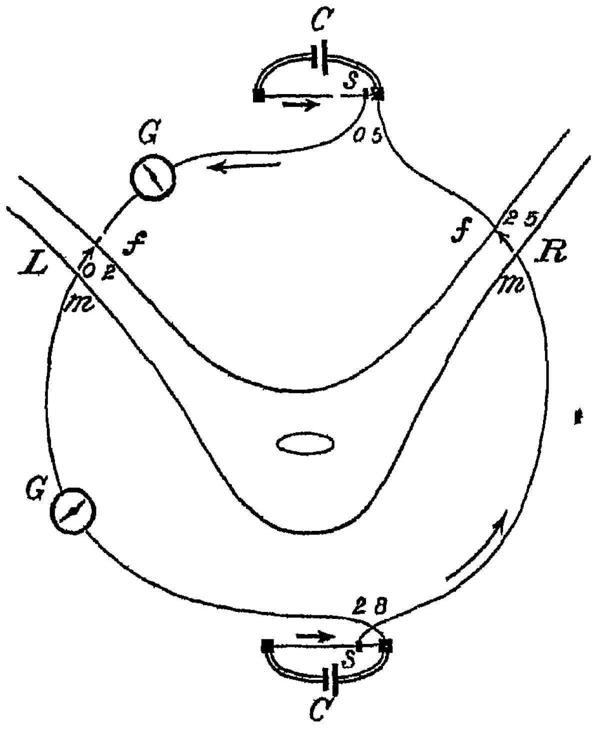
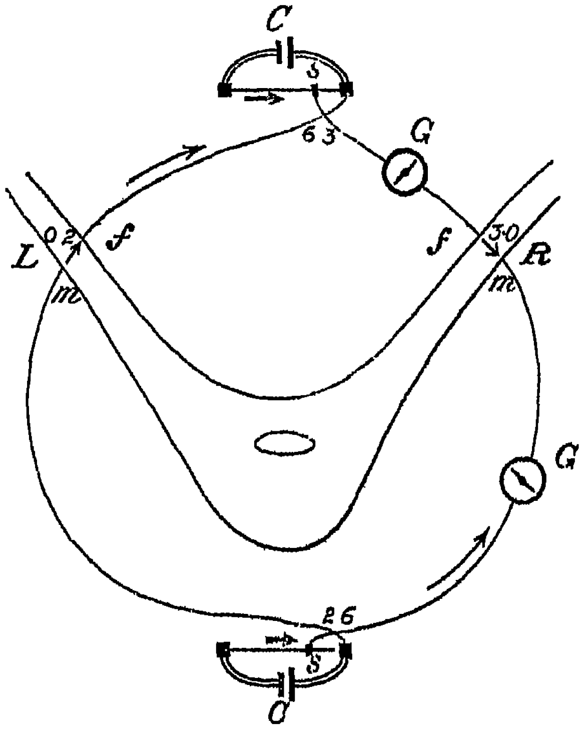


Diagram 8



The observation was so arranged that the opposite surfaces of either lobe could be connected with the galvanometer. As usual, these were found in very different conditions, but in both the direction of the difference was ↓, and in both the excitatory responses were those seen in unmodified leaves The galvanometer circuit was so arranged that it could be connected symmetrically either (1) with the two under surfaces or (2) with the two upper ones, that is, with the two spaces between the hairs on opposite sides. The condition of the leaf was carefully observed, and it was found that the state of things was, an hour or two after the leaf had been prepared, as represented by diagram 7. The upper surface of each lobe was positive to the under, but the difference was much greater on the right side than on the left, and the right under surface was positive to the left under surface. The current of a single Daniell's cell was now led for 10 seconds through the right lobe from *m* to *f*, and the process repeated six times in alternately opposite directions, with the usual result. On again investigating the condition of the leaf, it was found that, while the electrical relation between the under surfaces remained the same, that between the upper surfaces was reversed, the right having now become strongly positive to the left. On comparing the upper surface of the right lobe with the under surface, it was found about as much positive as it had before been negative The result will be best understood from the diagrams, in each of which the contour of a section of the lamina is indicated by the curved lines *f f* and *m m*.

C, C, C, C represent compensators, each of which is so arranged that by placing the slider, *s*, at the proper distance from the end block to which it is nearest, whatever current flows through the galvanometer in connection with it may be balanced so that the needle is at zero The number written near each compensator in diagram 7 expresses the length of wire which was required to balance the existing currents between the two under and the two upper surfaces respectively in the unmodified state, and the corresponding numbers in diagram 8 express the corresponding lengths after modification of the right lobe. Similarly, the numbers between *f* and *m* indicate the differences of potential between the upper and under surfaces respectively of the right and left lobe (*L* and *R*); in diagram 7 in the unmodified leaf, in diagram 8 after modification of the right lobe. The short arrows (at *L* and *R*) indicate the directions of the currents to be balanced, and the long ones those derived from the compensator wires. In diagram 7 the two upper surfaces are represented as nearly equipotential. In diagram 8 the upper surface of the right lobe, which has been modified, is strongly positive to the left. The relation between the under surfaces, *Lm*, *Lr*, remains practically unaltered. *Lm* is as much positive to *Rm* as it was before.

CONCLUSIONS AND SUMMARY OF RESULTS.

In the conclusions which were appended to my former paper I did not advance any theory of the relation which exists between the electromotive phenomena described and the property of responding by movement to mechanical or electrical stimulation which distinguishes the leaf of *Dionæa* from other leaves As, however, it is possible that I may not have the opportunity of resuming my investigations, it is perhaps desirable that I should no longer content myself with bringing together the bare results of my labours, but state as clearly as I can what their bearing appears to be on one of the most fundamental questions in physiology—that of the way in which the excitable protoplasm of plant or animal reacts when stimulated or injured.

With this view it seems to me necessary to place before the reader the notions which were until recently, if they are not now, entertained by botanical authorities on this subject; and I cannot do so better than by referring to the very full discussion of it contained in the 34th of Professor SACHS' Lectures on the Physiology of Plants, which were published a year after my last communication.*

Professor SACHS defines excitability as the property by virtue of which living organisms react to stimuli. This reaction, he says, is "physiological," not "physical," and belongs to "protoplasm"; and he emphasises the statement that the "phenomena of the effect need have no similarity or proportionality to the stimulus." "Excitable structures" he distinguishes as being "in a state of unstable equilibrium, of which every disturbance will sooner or later be compensated." The state of disturbance he characterises as a "new condition, that of excitatory action in which excitation can no longer be effective" Finally, he observes that in plants "the effects of excitation make their appearance slowly" . . "Several seconds, minutes, or even hours pass before the local excitation has traversed a path of 10, 20, or even 30 centims"

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* An English translation has recently been issued by the Clarendon Press, entitled 'Lectures on the Physiology of Plants,' by JULIUS VON SACHS; translated by H. MARSHALL WARD, M A, F L.S. Oxford, 1887.

As regards the leaf of *Dionæa* the definition with which Professor SACHS sets out holds good. There can be no question that the response of the leaf to stimulation is physiological, not physical, and that the effect is "disproportional" to the cause. But here correspondence ceases, and it becomes evident, from the subsequent passages in which he discusses the nature of the effect and its propagation, that he confounds with the physiological reaction the mechanical effects which the reaction eventually brings about long after it has itself ceased to exist The only effect of stimulation which Professor SACHS recognises is change of form—the only reaction, that of which change of form is the visible sign. What *we* mean by reaction or response to stimulation is a *molecular change*, which begins *immediately after its cause, and is propagated wherever there are continuous paths of excitable protoplasm*; and we recognise its existence, measure its duration, and determine the velocity with which it is propagated, not by the visible motions of organs which follow the reaction after long intervals of time, *but by the electrical disturbances which are their immediate concomitants.* The evidence that Professor SACHS, when speaking of propagation, means propagation of visible effects only, is to be found in such words as I have quoted as to the rate of propagation and the ineffectiveness of second stimulation. The highest rate of propagation which he recognises in plants is 10 centims in several seconds If by "several" we understand two or three, this would mean four centims. in a second. In *Dionæa* the rate is, at ordinary temperature, 20 centims. per second; that is, the local response takes place at a distance of 1 centim from the stimulated point 0″ 05 after the stimulus. Similarly, when Professor SACHS says that after a first stimulation a second is ineffectual, what he means is that, after the leaf of *Dionæa* has closed, after the leaf of *Mimosa* has drooped, or the filaments of *Cnicus* or *Centaurea* have straightened, they cannot undergo these several changes again until they have had time to resume their original form. But is it possible that Professor SACHS does not recognise that the reason why this is the case has nothing to do with protoplasm or its physiological reaction to stimulation? These movements cannot be repeated, not because the organ has thereby lost its excitability, but simply because for purely mechanical reasons repetition is impossible. It depends on the discharge of water from the constituent cells, and consequent loss of turgor, which cannot be reinstated until the cells have had time gradually to fill themselves again.

The purpose of Professor SACHS' remarks is to make it appear (1) that plants do not contain nerves, and (2) that there is nothing in them of the nature of nerves. As certainly as the first of these propositions is true, the second is mistaken The "nature" of a nerve is that it is excitable, that the effect of excitation is propagated, and that the excitation can be repeated immediately after with the same effect as the first time. So far as is known, the sole characteristic of this effect is that it is accompanied by electrical change, and its sole essential condition is that which was clearly indicated by NEWTON—continuity of substance in the channels of conduction.* In all these respects there is complete correspondence between the excitatory reaction in the protoplasm of the cells of the leaf and the excitatory reaction in nerve—the only difference being in the rate of propagation, and in the form and distribution of its paths. The difference of rate may be shown to be unessential by comparison with other examples derived from animal physiology In nerve the electrical change travels 100 times (30 metres) as fast as in the leaf (in which at high temperatures the rate of propagation is not less than 30 centims), in ordinary striped muscle about 10 times (3 metres) as fast, but in the muscular tissue of the ventricle of the heart of the Frog, at about half the rate (15 centims.). As no one doubts that in these three instances the process is essentially the same, the relatively slow propagation in *Dionæa* (enormously rapid as it appears as compared with Professor SACHS' standard) is unessential.

Having thus come to an understanding of Professor SACHS' theory (if it may be rightly so termed) of "irritability," all that remains is to inquire what his attitude is as regards the phenomena themselves. Does he deny them, or simply decline to recognise their bearing? The answer will be found in Lecture 37, in which, in commenting on my observations as to the electrical concomitant of the reaction, he sets forth his theory of its nature. Irritation produces migration of water—migration of water, electrical disturbance. He admits, therefore, the existence of an electrical disturbance consequent on excitation, but in accounting for it strangely disregards its time relations, forgetting that it has time to accomplish itself twice at least before its supposed cause comes into existence, and that its intensity is out of all proportion greater than that of the osmotic currents with which he identifies it. Happily, although some facts relating to the subject are perplexing, it is very easy for any one who has at his command the common appliances of a physiological laboratory, if he is not satisfied with my experiments, to observe himself all that is necessary to prove the impossibility of Professor SACHS' position.

It being once admitted that the excitatory process in the leaf is of the same nature as that which follows stimulation in animal structures, and more particularly in nerve, and organs belonging to the nervous system, there is reason for hoping that, just as the study of the excitatory process in animals affords a secure basis for its investigation in plants, so the relations we may be able to establish between observed phenomena in plants may guide us to the better understanding of corresponding relations in animals As was shown in the introduction, the question in animal physiology at present lies between those who regard the action of a stimulus as a mere interference with a previously existing state of electrical activity, and those who think that the electrical concomitant of excitatory reaction has no necessary connection with any such state. According to the former view, it is held that when a muscle is excited the excitatory variation comes into existence *d'emblée*, according to the latter, the constant operation of one or more such forces is presupposed, as well as their liability to be disturbed by external influences. In the leaf, observed facts show most conclusively that the two sets of phenomena—those of the excited and those of the unexcited state—are linked together by indissoluble bands; that every change in the state of the leaf when at rest conditionates a corresponding change in the way in which it responds to stimulation, the correspondence consisting in this, that the sign, that is the direction, of the response is *opposed* to that of the previous state, so that as the latter changes sign in the direction from ↑ to ↓ the former changes from ↓ to ↑.

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* See query 24 at the end of Book III. of the "Optics," HORSLEY'S Edition of 'NEWTON'S Works,' vol 4, p. 226.

This remarkable relation, the discovery and experimental demonstration of which has been the most important fruit of my more recent work, can only be understood to mean that the constantly operative electromotive forces which find their expression in the persistent difference of potential between the opposite surfaces, and those more transitory ones which are called into existence by stimulation, have the same seat—the opposition between them being in accordance with the general principle that, whereas the property which renders a structure capable of undergoing the excitatory change is expressed by relative *positivity*, the condition of discharge is expressed by relative *negativity*.

Much light is thrown on the relation between the excitatory reaction (action current) and the previous difference (leaf current) by the observation of the influence exercised on both by external voltaic currents. We have seen that when such a current is led through a leaf for a very short period it produces a lasting effect, which is always in the same direction, that of the excitatory reaction, whatever may be the direction of the external current. But this influence is exercised more effectually when the direction of the external current is descending (that is, when it coincides with that of the effect to be produced) than when it is ascending. In animal structures analogous to the leaf, and particularly in the electrical organ of the Skate or Torpedo, we find the direction of the lasting effect of a current led across the disks or plates to be always normal, whatever may be that of the current itself—*i.e.*, that of the natural discharge of the organ; but a homonymous current is much more effectual than one in the opposite direction. In the application by DU BOIS-REYMOND of the term "positive polarisation" to the after effects of voltaic currents led through muscles and nerves, a similar relation is suggested, which, however, is complicated by other conditions which cannot be here discussed. But in the leaf, as in the electrical organ, the relation admits of being very simply stated, and in the same terms for both. The sub-excitation which the external current leaves behind it operates always in the same direction, its intensity, not its sign, being dependent on the direction of the current which has produced it

As regards the localisation of the electromotive changes which are associated with "modification" and "excitation," we have given experimental evidence that they have their seat at or near the upper surface of the lamina. Accepting the principle already formulated, that all such action depends on difference of physiological activity between adjacent cells or strata of cells, provided that their protoplasms are in continuity, we may account for the phenomena observed, by supposing that in the unmodified state the most superficial strata are positive to those subjacent to them, and that the effect of sub-excitation, as well as of the excitatory explosion, is to diminish, annul, or reverse this difference, so that eventually the excited superficial cells become less susceptible of excitatory change—the result being that the excitatory variation, which in the unmodified state may be compared to a contest between opposing electromotive forces, assumes the decisive character which belongs to modification. Without venturing to say that this is precisely the way in which the result is brought about, it seems clear that the process of modification may be rightly compared to a contest between two electromotive actions, of which the one represented by the ascending arrow (↑), at first predominant, eventually yields to the other (↓)

By way of conclusion, I propose to state in the shortest language the experimental facts which have been established.

1 In the leaf of *Dionæa*, in its prime, the upper surface is positive to the under. On excitation it becomes suddenly negative. This change, constituting the first phase of the excitatory variation, occupies for the most part the first second after excitation. It is often preceded by a momentary change in the opposite direction.

2. Subsequently it undergoes a gradual change, which is designated in the experimental part of the paper by the term "modification" This consists in diminution of the negativity of the upper surface, and its eventual replacement by relative positivity. The change is accompanied by (*a*) reversal of the sign of the excitatory variation, (*b*) (later) by diminution of the electrical resistance of the leaf.

3. The first phase of the excitatory variation is followed both in the modified and unmodified state of the leaf, provided that it has not been excited immediately before, by an after effect which has always the opposite sign. If the leaf has been excited immediately before, the second phase is absent.

4. Modification may be produced at will by passing a voltaic current for a very short period through the leaf in either direction, even though the current be so weak that its closure is not followed by an excitatory variation. It is a local effect which is not propagated. One lobe may be modified without the other, and even one part of a lobe without the surrounding parts.

5. The propagated excitation reaching a part of the leaf which has undergone

modification evokes a modified response of which the direction of the first phase is ascending, and a response of the opposite sign in the unmodified region.

Two questions, among others, may be mentioned as requiring further investigation. One relates to the cause of the diminution of electrical resistance which accompanies the process of modification, particularly its relation to the disappearance of turgor. The other concerns the process by which the modified part regains its pristine state, and the time required for its accomplishment. To these I shall give attention, if opportunity offers.

My thanks are due to Mr. F. GOTCH for his able assistance in the experiments recorded in this Paper, and to Messrs. F. J M. PAGE and G. BURCH for their aid in the photographic observations.

EXPLANATION OF PLATES.

PLATE 69.

Figs. 1 to 4. Photographic records of the "Fundamental Experiment" in different leaves. (See 'Phil. Trans.,' 1882, p. 25.) The leaf is excited at intervals of about 5″ by a single induction shock led through the opposite lobe at the moment indicated in the photograph by the break in the bright line. As the make induction shock was cut off, the moment of excitation corresponds to the right-hand edge of the interruption. Figs. 1, 3, 4 are at ordinary temperature, fig. 2 at a high temperature (25° C.).

Fig. 5. Same experiment as fig. 3. Leaf exhausted.

Fig. 6. The same experiment. Interval between the excitations prolonged; hence the second phase of the response, which is usually only observed after the first excitation, here occurred after the second.

Fig. 7. The same experiment. Mechanical, instead of electrical, excitation. Double effect, due to accidental touching of two sensitive filaments one after the other.

PLATE 70.

Fig. 8. Experiment described in 'Phil. Trans.,' 1882, pp. 32–38; the leaf was led off by corresponding points on the under surface of opposite lobe. The tracing shows the combined result of opposite electromotive changes taking place in the two lobes. Leaf excited mechanically on right side.

Fig. 9. The same leaf excited alternately on right and left sides.

Fig. 11. Photographic record of the "fundamental experiment" in a perfectly "unmodified" leaf.

Fig. 12. Effect as led off from the same contacts in the same leaf after "modification" [The photograph shows an imperfection, due to a temporary defect in the electrometer. The first of the four notches ought to have been deeper.]

Fig. 13. Effect often observed in leaves just prepared. It corresponds to a state intermediate between figs. 10 and 11.

N.B.—In all cases the difference was compensated just before the observation was made.

XVII. *On the Modifications of the First and Second Visceral Arches, with especial reference to the Homologies of the Auditory Ossicles*

By Hans Gadow, *Ph.D., M.A., Strickland Curator and Lecturer on the Advanced Morphology of Vertebrata in the University of Cambridge.*

Communicated by Professor M. Foster, *Sec. R. S.*

Received April 12,—Read April 26, 1888

[Plates 71–74.]

An ample material of rare Elasmobranch forms, especially *Heptanchus, Hexanchus, Centrophorus, Myliobates,* and *Trygon,* which I had collected during the last summer on the South Coast of Portugal, and several fresh specimens of *Hatteria,* have induced me to submit the question of the modifications of the two first visceral arches to a reconsideration.

The homologies of the auditory ossicles have not hitherto been settled beyond dispute, and only recently this question has again been taken up by Albrecht, Dollo, Bauer, and Gradenigo. The most important of these latest contributions has been made by Albrecht, who, chiefly for theoretical reasons, advocates that the whole of the auditory chain in all the Amphibia and Amniota is homologous with the hyomandibula of the Fishes.

However, since one of his premisses is highly disputable (quadrate = processus tympanicus of the os squamosum), and considering that one of his principal conclusions leads to a complete and absolutely unjustified reversion of the views which are generally accepted regarding the morphology of the visceral arches, his conclusions as to the homologies of the auditory ossicles have never met with any favour. I trust, therefore, that my attempt to reconsider the whole question on the broadest basis will not be superfluous.

Nearly all the preparations figured in this essay are in the Cambridge University Museum of Zoology and Comparative Anatomy.

Heptanchus cinereus.—The second visceral, or hyoidean, arch consists of a hyomandibular bar, a hyoid bar, and the copula. The whole arch is very slender, especially the level of the masticatory joint, and is almost completely hidden from a side view by the first visceral arch.

The connexion of the hyomandibula with the cranium is not effected by articulation, but by distinct and strong ligaments. One of these ligaments arises from the labyrinth region of the cranium, above and slightly in front of the exits of the facial and glossopharyngeal nerves, it is attached to the upper, or proximal, and anterior end of the hyomandibula. The second ligament is much longer, a strong, white, roundish band, which arises somewhat more forward from the lateriventral aspect of the vestibular process of the labyrinth region, and is attached to the anterior margin of the hyomandibula, somewhat above its middle. Between this ligament and the hyomandibula passes out to the posterior side of the arch the hyoidean division of the facial nerve.

The proximal end of the hyomandibula is connected also by one ligament with the upper corner of the ceratobranchial or second segment of the third visceral arch (first branchial arch), and by a similar ligament with the outside of the middle of the epibranchial of the same arch.

Whilst in *Heptanchus* there is hardly any articular facet on the proximal end of the hyomandibula, and only a very slight depression on the corresponding surface of the cranium, there is in *Hexanchus* a more distinct indication of a primitive articulation, although, owing to the intervention of the ligaments described, no absolute contact seems to take place.

The hyomandibula of *Heptanchus* passes down the median side of the very massive quadrato-palatine bar, is partly lodged in a slight excavation of this bar, and passes into the likewise very slender proximal end of the hyoid bar. The junction between these two elements is just as primitive as those between the various segments of the branchial arches. The second visceral arch is partly lodged in slight excavations of the quadrato-palatine and mandibular bars; the hyoid-hyomandibular junction rests against the hinder surface of a prominent knob, which forms the medial or inner quadrato-mandibular articulation. The only direct connexion between the first and second visceral arches is formed by a ligament which arises from the inner side of that mandibular knob, and is attached to the anterior brim of the end of the proximal third of the hyoid (fig. 1A, Plate 71).

The quadrato-mandibular junction exhibits some very important points. There are two articulations, separated by an empty space. Both articulations belong to the cup and ball type. On the outer or posterior articulation the ball is formed by a broad knob of the quadrato-palatine bar, fitting into a slight concavity of the posterior and outer end of the mandible. The inner, or anterior, articulation is formed by a roundish protuberance of the mandible which fits into a concavity of a corresponding process of the quadrate portion. This latter articulation is, so to speak, not yet completely finished, because in the angle between quadrate and mandible both these segments go over into each other by a thick portion of hyaline cartilage (fig. 1B*). Unless we assume that this continuation was once a ligament, which was later on converted into cartilage, we have to conclude that the quadrato-mandibular joint, this oldest of visceral joints, is not yet completed, and still partly represents, by the continuation of its two component segments, the primitive stage which we have to assign to the originally unbroken visceral arches.

Oxyrhina gomphodon (fig. 3).—This Selachian shows a great step in advance towards higher Elasmobranch conditions, and exhibits far less primitive conditions than the Notidanidæ The quadrato-palatine bar no longer articulates by a broad and long concave facet with a post-orbital process of the cranium, so conspicuous a part in the cranium of *Notidanus*, but has lost this cranial connexion entirely. It is connected with, and is supported entirely by, the mandible. There are likewise an outer and an inner articulation, but, instead of the hyaline cartilaginous continuation of quadrate and mandible, there are now two partly fibro-cartilaginous ligaments, which cross each other—one, ligamentum quadrato-mandibulare internum superficiale; and the other, lig quad.-mand. int profundum The great points of interest which mark the step in advance towards higher conditions are the formation of two distinct articulations of the mandible with the hyoid, and the formation of four new ligaments, by which an intimate morphological and physiological connexion between the first and second visceral arches is effected.

The two articulations between the mandible and the hyoid are these —The mandibular knob on the inner quadrato-mandibular articulation, against which in *Heptanchus* leans the proximal end of the hyoid, is in *Oxyrhina* greatly enlarged into a medially and upwards directed thick process, against which leans firmly the anterior surface of the top end of the hyoid, there is developed even a distinct glenoid surface. On to this mandibular knob is attached, moreover, a weak ligament, which comes from the connective tissue which surrounds the hyomandibular-hyoid junction, most of the fibres of this ligament come, however, from the inner side of the lower end of the thick and blunt hyomandibula. This ligament is therefore a lig. hyomandibulo-mandibulare.

The second articulation between mandible and hyoid is effected by the posterior surface of the outer mandibular process of the quadrato-mandibular articulation; a slight depression on the mandible receives a knob of the hyoid, as is shown in fig. 3*b*. Above and below this primitive articulation are three strong and short ligaments, to be distinguished as lig. hyoideo-mandibulare laterale inferius, lig. hd-mand. lat. superius, and lig. hyoideo-mandibulare mediale. The latter ligament is attached to the inner aspect of the mandible near the brim of its broad rounded-off portio angularis, and comes from the lower side of the articulatio hyoideo-mandibularis externa, just described. From this point of attachment to the hyoid, it is, however, continued around and over the inner surface of the hyoid, and splits up into two strong strands, one of which is attached to the posterior edge of the hyomandibula, a little below its middle, whilst the other strand passes on the medial side of the hyomandibula to the under surface of the cranium, far in front of the articulation of the hyomandibula with the cranium. Thus a connexion between the hyoid and the cranium, and, although indirectly, of the latter with the mandible, is effected. The sole ligament which connected the hyoid with the mandible in *Heptanchus* is absent in *Oxyrhina.*

The hyomandibula is attached to the cranium and to the first branchial arch by the same three ligaments, as in *Heptanchus*; but, in addition to them, it articulates with the cranium by a well-developed cup-and-ball joint

Lastly, we observe that the second visceral arch, which, besides still carrying a gill, has assumed the function of suspending or carrying the first arch, is very strong and thick; its two principal components, the hyomandibula and the hyoid, articulate with each other, behind by two knobs, and in front by two concave facets, between which is placed a round piece of fibrous cartilage, held in its place by, and partly imbedded in, connective tissue (fig. 3 *c.*). The suspensorium in *Oxyrhina* is consequently formed chiefly by the hyoid.

Sphyrna zygæna (fig 4).—The first visceral arch is comparatively weak, the palato-quadrate bar is, in fact, several times thinner than it is in *Oxyrhina,* and still weaker than in *Heptanchus.* The second arch is very strong. The thick and long hyomandibula articulates with the skull, and has the same ligaments (cranial and branchial) as have the two previous types. The long ligament from the under surface of the cranium, connecting the latter in *Oxyrhina* with the hyoid and mandible, after having received a band from the hyomandibular, is likewise present in *Sphyrna,* but, as the drawing shows, the direction of the angles formed by these ligaments with the parts to which they are attached is reversed.

The lig. mandib. hyoid internum, absent in *Oxyrhina,* is present in *Sphyrna,* as in *Heptanchus.*

The inner big knob of the mandible, near the inner or median quadrato-mandibular articulation, articulates with its slightly rounded anterior surface against a distinct concavity of the posterior surface of the proximal end of the hyoid. The lig. hyomandibulo-mandibulare is, as in *Oxyrhina,* attached to the sustentaculum of the mandible, but it is very strong in *Sphyrna,* and arises chiefly, or almost entirely, from the hyomandibula itself. A new and strong ligament, hitherto not observed, connects the posterior side of the hyomandibula with the outer and anterior surface of the quadrate. From this point of attachment arises a long ligament which crosses all the others in going to the inner surface of the neck of the mandible: it is a lig. quadrato-mandibulare internum.

There are in *Sphyrna* none of the three ligg. hyoideo-mandibularia described in *Oxyrhina.*

Centrophorus (fig. 2).—In half-ripe embryos the hyomandibula articulates by a rather shallow facet with the cranium, and the whole second arch is considerably less bulky than the first arch, the quadrate region of which no longer articulates with the cranium. In the adult the second arch has become more bulky than the first arch, and the hyomandibula has formed a roundish big knob, which is received into a deep cavity of the labyrinth region; it is there connected with the cranium by loose ligamentous tissue, which surrounds the whole of the articulation. There are no distinct ligaments connecting the hyomandibula with the ventrilateral surface of the cranium, or with the first branchial arch. There is, however, a ligament which connects the posterior border of the proximal end of the hyoid with the posterior border of the middle of the hyomandibula, whence ligamentous tracts, together with the perichondral sheath, can easily be traced upwards to the cranium, near the posterior brim of the articulation. Thus, this tract corresponds with the posterior hyomandibular-hyoidean ligament of *Oxyrhina* and *Sphyrna*, and, to a certain extent, with the ligamentous cranio-hyoidean connexion of the same types

From the anterior knob of the distal end of the hyomandibula goes a strong fibro-cartilaginous ligament to the sustentaculum of the mandible, and from this sustentacular or hyomandibulo-mandibular ligament goes a weak, ligamentous string to the neighbouring surface of the hyoid. This string, which we will call the *lig. intermedium*, corresponds with one of the ligg. hyoideo-mandibularia interna of other Selachians Another lig. hyoid.-mandib., more distal, and somewhat stronger, is likewise present. The quadrate articulates with the mandible only by one (lateral) facet; the inner knob of the mandible is used for the articulation of the mandible with the hyomandibula and the hyoid. This articulation is, however, not a direct one, because the sustentacular knob of the mandible is separated from the two elements of the second arch by the cross-ligaments, as seen in fig. 2. Lastly, there is a long and strong lig. quadrato-mandibulare internum.

The suspensorial apparatus of *Centrophorus* presents, therefore, features which in many points are less advanced than those of either *Oxyrhina* or *Sphyrna*, although, as in these, the autostylic condition of the Notidanidæ has already been superseded by a hyostylic arrangement, with the additional suspension of the palatine bar from the cranium by a broad and strong, but loose, ethmo-palatine ligament.

Concerning *other Selachians*, I may be permitted to refer to some of GEGENBAUR'S observations. The ligament which extends from the cranium along the anterior margin of the hyomandibula, and attaches itself to the anterior and inner surface of the mandibular process of this cartilage, is very strongly developed in *Mustelus* and *Galeus*. Of other ligaments, we find in the same genera and also in *Scyllium* the lig. hyomandibulare posterius, exactly as we have described it in *Centrophorus*, and, with modifications, in *Oxyrhina*. As in the latter form, this ligament is in *Mustelus* and *Scyllium* continued on to the mandible (our lig. hyoideo-mandibulare mediale; GEGENBAUR'S äusseres Hyomandibularband, p. 169). His inneres Hyomandibularband is our lig hyomand. mand. internum, *s.* lig. sustentaculi. Besides these, he describes a lig. hyomand. hyoideum anterius, which connects the lateral surface of the distal hyomandibula with the anterior proximal surface of the hyoid; it prevents the hyoid from contact articulation with the sustentacular knob of the mandible.

Whilst, therefore, in *Mustelus* and *Scyllium* there exists no immediate articulation between the hyomandibula and the mandible, GEGENBAUR found that in *Acanthias* the sustentacular or inner hyomandibular ligament sends a broad fibro-cartilaginous process to the sustentaculum, which process then acts as an interarticular cartilage disk between the mandible and hyomand. This arrangement is carried further in *Galeus* (sp ?). The mandible articulates with the hyomandibula, and in the articular cavity is placed a pure cartilaginous disk, which is held in its place by a capsular ligament.

In *Scymnus* and *Cestracion* the hyomandibula articulates directly with the mandibular sustentacular knob, without the interference of cartilage, although the same ligaments as in *Mustelus* are present, but in a modified form.

Torpedo (fig. 6).—The quadrato-palatine and the mandibular bars are both very slender, and exhibit no processes whatever by which these elements in the Selachians are eventually connected with either cranium or hyoid.

The hyomandibula is an enormously broadened-out plate of a more or less triangular shape. Its basis is straight and articulates throughout its length with the cranium. There are no special ligaments developed. On the anterior irregular margin of the hyomandibula rest, and are loosely connected with it, two spiracular cartilages. That, and how, these elements—which originally belonged to and were carried by the palato-quadrate bar—gradually give up their original connexion and become attached to either the cranium or to the hyomandibula, has been fully explained by GEGENBAUR ('Kopfskelet,' pp. 197–205).

The posterior proximal end of the hyomandibula articulates with the proximal end of the first branchial arch. The hyoid articulates with the middle of the posterior margin of the hyomandibula. The distal end of the latter is connected by a thick and strong fibrous ligament with the sustentacular end of the mandible. Inside this ligament is enclosed an irregularly-shaped nodule of fibrous cartilage. This nodule is not circumscript, but passes gradually into the surrounding fibrous tissue of the ligament, after the manner of a sesamoid bone. The quadrate articulates with the mandible by a well-formed double joint, but there are no distinct ligaments. In fact, the strong hyomandibulo-mandibular ligament is the only one to be noticed.

Trygon (fig. 5).—In comparison with *Torpedo*, we find in *Trygon* a more complicated arrangement, which combines certain higher advanced features with the unmistakably retrograded, and therefore simpler, structures of the former type. The hyomandibula is by far less broadened out, and preserves the shape it has in most Selachians. It is placed in an almost horizontal position. Its proximal end articulates with the cranium and sends out a process towards the exit of the glossopharyngeal nerve; this process is likewise used for the cranial articulation. Immediately behind this process, leans on to it, and at the same time with a facet on to the cranium, the very slender hyoid bar. Special ligaments, connecting the hyoid with the hyomandibula, no longer exist, nor is the hyoid, now so far removed from the first visceral arch, in any way connected with the latter.

This cranial attachment of the hyoid behind the hyomandibula is of great importance concerning our investigations. This cranial connexion of the hyoid, going hand-in-hand with an absolute removal from the first visceral arch, is, as GEGENBAUR has shown, not owing to a migration of the hyoid upwards towards the cranium, but, firstly, to an arrest or retrogressive development of the proximal end of the hyomandibula, and, secondly, to considerable development of the sustentacular portion of the distal half of the hyomandibula. The longer this sustentacular portion becomes, the more the upper end of the hyoid bar will appear removed from the neighbourhood of the quadrato-mandibular and hyomandibulo-mandibular articulations; the ligaments which in previous types connected the hyoid with the first arch will gradually be given up, and a stage will be reached in which, as in *Torpedo*, the hyoid appears attached to the hyomandibula half-way between the masticatory joint and the cranium. In a further stage the cranial or upper portion of the hyomandibula will be still less developed, and the hyoid almost touches the cranium GEGENBAUR mentions these important facts ('Kopfskelet,' p. 173). "The separation of the hyoid from the hyomandibula is completed in the other Rays (except in *Torpedo*) The hyomandibula there retains only its relation to the mandible; it becomes the bearer of the jaw-apparatus, whilst the hyoid henceforth behaves as the branchial arches. It is, in this case, either still attached to the cranium, as in *Rhyncobatus*, *Trygon*, and *Myliobates*, or it has become free, as in *Raja*. In either case its features are those of a branchial bar. The separation of the hyoid from the hyomandibula is, however, not quite complete even in these cases, because there is still a ligamentous connexion, which is traceable even in *Raja*. In *Rhyncobatus* and *Pristis* I find an articulation, close to the cranium, between the hyomandibula and that part of the hyoid which is attached to the cranium."

The articulation of the hyomandibula with the two jaws is, in *Trygon*, effected in the following way:—(1.) A complete articulation of the hyomandibula with the posterior border of the upper jaw; above this joint is found a small cartilage. (2.) A less complete articulation between the hyomandibula and the mandible. (3.) Articulation of the hyomandibula with the under jaw, not directly, but interfered with by the following ligaments:—

A strong lig. hyomandibulo-mandibulare. This encloses a piece of cartilage, like that in *Torpedo*. From this strong fibro-cartilaginous ligament goes a thinner one to the middle of the anterior or upper margin of the under jaw. It likewise contains a piece of cartilage. The quadrate bears a distinct convex knob, which fits into a facet borne by the inner mandibular articular process. In opposition to *Centrophorus*, there is in *Trygon* an inner, and not a lateral, jaw articulation of the two jaws, and whilst in *Centrophorus* the inner or sustentacular knob is used for the direct contact articulation with the hyomandibula and hyoid, the hyomandibula in *Trygon* comes into contact with the mandible only behind the sustentacular ligament.

I. In summing up with respect to the Elasmobranchs, we find that the first and second arches do not at all articulate with each other in the Notidanidæ, that a suspensorial arrangement is found in all the others, but that this does not lead to a direct contact articulation in *Centrophorus*, *Mustelus*, and *Acanthias.* Again, in *Oxyrhina* and in *Sphyrna* the hyoid and mandible have developed articular facets for contact, whilst the hyomandibula does not do so. Contact between the hyomandibula and the mandible takes place in *Galeus, Scymnus, Cestracion* and *Trygon.* Lastly, in *Trygon* we have contact also between the hyomandibula and the quadrate portion of the first arch.

II. With regard to the hyoid bar, this becomes more and more removed from the jaws until it reaches the cranium, and lastly is firmly attached to it, behind the hyomandibula, in certain Rajidæ, notably in *Raja*, *Myliobates*, and *Trygon.* The hyomandibula is invariably attached to the labyrinthic region of the cranium and articulates with it.

III. With regard to ligaments, we find that with the exception of capsular ligaments at the masticatory joint, the only constant one is the lig. hyomandib. mandibulare internum, *s.* lig. sustentaculi. This is phylogenetically very early developed; it is, in fact, found in all the cartilaginous Fishes above the Notidanidæ. This ligament, moreover, frequently contains fibrous and even hyaline cartilage, *e.g.*, in *Galeus, Trygon, Torpedo.*

There exists not unfrequently a ligamentous connexion between the labyrinthic region of the cranium and the proximal end of the hyoid element, *e.g.*, in *Oxyrhina, Centrophorus, Sphyrna, Trygon, Raja;* and these ligaments are certainly not the remnants of cranio-hyoidean muscles, although they sometimes (*Oxyrhina*) do serve as additional supporters of muscular fibres.

Ceratodus.—The massive first visceral arch is divided into three parts, the upper bar being differentiated into a palatine and a quadrate element. The latter is fused with the cranium by its proximal broad end, and therefore resembles the conditions met with in other holostylic skulls, as, *e.g.*, in *Cestracion* and *Chimæra.* The distal end of the quadrate articulates by a concave surface with a convex knob of the mandible. There is no contact or articulation of the lower jaw with the second visceral arch. The hyomandibula is represented by a small irregularly shaped cartilage, which is attached to the labyrinthic region of the cranium and to the neighbouring quadrate. It sends a small conical process outwards and downwards. In this process we recognise the suspensorial portion of the Elasmobranch hyomandibula, and HUXLEY compared it with the symplectic element of Teleostean Fishes.

The outer surface of this hyomandibular remnant is loosely connected with the small cartilaginous operculum, which we know to be the result by fusion of the branchiostegal rays, carried by the hyomandibula.

Of ligaments the following are important .—

1. Lig. hyomandibulo-hyoideum = HUXLEY's hyosuspensorial ligament. It arises with a broad basis from the lower surface of the hyomandibula and the cranium, and is attached to the broad top end of the club-shaped hyoid. Imbedded in this ligament

is the conical process mentioned above. The whole ligament represents undoubtedly the anterior and posterior hyomandibular-hyoidean ligaments of Elasmobranchs, and it has still preserved the cranio-hyoidean connexion.

2 Lig. hyoideo-mandibulare. A strong and round ligament, which connects the anterior proximal surface of the hyoid with the posterior proximal end of the mandible, closely behind its articulation with the quadrate. Owing to the fusion of the quadrate with the cranium, and owing to the large downward extension of the quadrate, the second visceral arch in *Ceratodus* is dispensed with as a suspensor of the jaws, and the existing few, but strong, ligaments connecting the two arches mainly serve the purpose of holding the hyoid in its place, instead of, as in most Elasmobranchs, holding and supporting the first arch.

The hyomandibula has lost its important function, and persists now as a degenerated piece of cartilage, which is, so to speak, shoved into a dead corner by its overgrowing neighbour, the quadrate However, it still preserves its original connexion with its distal paramere, the hyoid.

We are not permitted to look upon the arrangement of the arches of *Ceratodus* as more primitive than those of any Elasmobranch, on the contrary, we have to derive it from an amphistylic, and this, of course, from a simple autostylic, form.

It is highly probable that in the ancestral *Dipnoi* the hyomandibula was much larger, and that it was already, as in Teleosteans, broken up into a proximal cranial persisting part, and into a distal or symplectic element, which later on, when the hyostylic support of the jaws was superseded, either persisted (*Proteus*, &c.), or ultimately became lost (*Ceratodus, Salamandrina*)

Urodela.—In *Siren* and *Menopoma*, the hyomandibula is about as much, or rather as little, developed as in *Ceratodus*, and it is partly confluent with the periotic and quadrate cartilage In *Proteus* there is besides a " stapes " (see fig. 8), a large piece of cartilage which is with its extended top attached to the lower edge of a large fascia. This fascia runs along from the upper part of the " suspensorium," behind and beneath the stapes, and is attached to the inferolateral face of the epiotic (PARKER). This broad ligament (PARKER's suspensorio-stapedial ligament) is the same as that in *Menobranchus.* There is also a ligament which runs from the hyomandibula and upper end of the hyoid to the quadrate, this ligament corresponds with the two in *Menobranchus;* lastly, there is the usual hyoideo-mandibular ligament. Whilst PARKER calls the broad piece of cartilage of *Proteus*, which, according to him is absent in *Seironota perspicillata,* and probably is absent also in *Siredon* and in *Amblystoma*, the hyomandibula proper, and thinks ('Urodela,' p. 554) that the " stapes is cut out from the preformed cartilage of the ear-capsule," it seems to me more probable that PARKER's hyomandibula of *Proteus* and of other Perennibranchiata is the distal segment of the hyomandibula, comparable to a symplectic, whilst the " stapes " is the proximal portion of the original hyomandibula, which is now broken up into two pieces. If this symplectic or distal cartilage disappeared in *Proteus*, this creature would present almost exactly the same features as *Menobranchus*. That we are justified in postulating the disappearance of the distal part of the original hyomandibula, is shown by *Siren* and *Menopoma*, in which this same cartilage is scarcely one-fourth the size of that of *Proteus*, and is moreover confluent with the quadrate. Lastly, such a cartilage appears no longer in *Seironota perspicillata* (PARKER).

This conception of the hyomandibula is strengthened by the fact that PARKER himself is not clear about the origin of the whole "stapes." His first suggestion that the stem of the stapes in *Menopoma* is equal to the annulus tympanicus of the Frog is to be found in his work on the Urodela, p. 559, foot-note. On p. 587 he says :—"By the time the tail has disappeared in the Frog, the primary otic process has become a free trifoliate 'spiracular cartilage'; this becomes the cartilaginous annulus tympanicus, it is always, at any stage, above the portio dura nerve. In certain Urodela (*Menopoma, Spelerpes, Desmognathus*), the two latter being Caducibranchs, this cartilage grows to the stapes, and generally fits its narrow posterior end into a cup-shaped process of the stapedial bony centre; in some it is independently ossified and free These two specialisations of that peculiar Selachian spiracular cartilage are of great interest, suggesting the possibility of many curious transformations of ichthyic elements in the higher classes."

Now the very circumstance that this otic process is always situated above, *i.e.*, dorsally from and anterior to the facial nerve, shows that it cannot become the stem of the stapes, because the ossicular chain is invariably situated behind and inwards from that nerve. On the contrary, the long outgrowth of the otic process gives rise to the long suprastapedial element of certain Anura; the base of this element forms the annulus tympanicus, whilst its distal end is attached to the lateral end of the ossicular chain, and can in time become fused with it.

Menobranchus (fig. 7).—The first visceral arch, with the addition of a well-developed squamosal bone, and the hyoid bar resemble that of *Ceratodus*.

The hyomandibula is removed from contact with the quadrate; it is much smaller than it is in *Ceratodus*, and, moreover, its base is broadened out into a round disk, which is firmly wedged into a corresponding foramen of the otic region. This foramen corresponds with the fenestra ovalis, and the hyomandibula itself has assumed a stapes-like form. It has entered a new service, namely, that of the whole auditory apparatus.

Of ligaments there are four, which it is easy to compare with those of the Dipnoi and Elasmobranchs, provided we take into account the changes which must have been produced by the development of a long and independent quadrate, together with a corresponding withdrawal and reduction of the hyomandibula.

Ligaments:—1. Most medially placed is a broad fibrous ligamentous connexion of the proximal end of the hyoid with the quadrate, and with the whole brim of the cranium from the distal end of the quadrate to the base of the hyomandibula.

2. A lig. quadrato-hyoideum = HUXLEY's hyosuspensorial ligament, arising from the posterior side of the middle of the quadrate and the adjoining part of the cranium.

3. A strong fibrous bundle from the lower surface of the hyomandibula, and with a few fibres from the cranium to the middle of the quadrate. The hyoid branch of the facial nerve passes above this hyomandibulo-quadrate ligament, *i. e.*, in front of the hyomandibula and behind the quadrate. This ligament is, therefore, in the same relative position to other parts as is the anterior cranio-hyomand lig. of many Selachians, and this comparison becomes still more obvious if we look upon the 2nd and 3rd ligaments of *Menobranchus* as equivalent to the ligamentous connexion between the cranium, hyomandibula, and mandibula in *Oxyrhina*, and with the quadrate region in *Sphyrna*. At any rate, the broad medially-situated 1st ligament contains potentially all the possible connexions between the cranium, hyomandibula, quadrate, and hyoid. Ligaments 2 and 3 are to be looked upon as differentiations of the lateral tracts of a hyomandibulo-hyoidean connexion which, because of the reduction and withdrawal of the hyomandibula, have obtained a hold upon the quadrate, and this has led to the formation of two apparently new ligaments.

4. A lig. hyoideo-mandibulare.

Anura.—The larva of *Pseudis paradoxa*, described and figured by PARKER, exhibits an arrangement almost the same as that in *Menobranchus*. The symplectic half is absent. The stapes, with a pillar-like extension, the "columella," turns towards a tympanum, which, like the tympanic ring and the whole auditory capsule, is highly developed. The auditory cartilages are not connected with either quadrate or hyoid. The hyoid bar itself does not reach the cranium, but is fastened to the posterior side of the quadrate by a broad ligament.

In most of the Anura, however, this connexion is given up, and, instead of this, the proximal end of the hyoid is attached to the cranium, either by short ligaments, or it may even be fused with the cranium, as in the adult of *Pelobates* or in *Bufo*. The hyoid in these cases resembles that of the Rajidæ. The fact that the point of the cranial attachment of this "stylohyal" varies, indicates that it is a feature which was acquired after its separation from the hyomandibula or ossicular chain had taken place inside the Anurous group. We can, therefore, not be astonished to find the stylohyal end attached to any of the neighbouring cartilages or bones, which lend it the support required. The auditory chain of *Pelobates* and *Otilophus* (fig. 9B) is very simple; it is let into the fenestra ovalis by a stapedial disk; this passes into a straight or a curved slender rod (mediostapedial), the outer end of which is bent downwards (extrastapedial), and is attached to the middle of the tympanum. There is no attachment of the fenestri-tympanal elements with either mandible, quadrate, or hyoid. ALBRECHT's "figure schématique," in which he represents the Amphibian ossicular chain as connected with the mandible, is not supported by facts (*cf.* his paper on the Eustachian tube, fig. 10, p. 22).

Just as the hyomandibula of Fishes can break up into two parts, this fenestri-tympanal cartilage can become jointed at various places. The most frequent joint is that between the basal or fenestral disk and the stem or rest of the rod; the latter is then conveniently spoken of as the columella auris, or this columella may break up again, and form an inter-, medio-, and extra-stapedial piece. ALBRECHT therefore distinguishes between "Amphibiens columellifères" and "Amphibiens ossiculifères"—*e.g.*, *Rana pipiens* (fig. 9A), *R. halecina*, *R. pygmæa*, according to PARKER. These Anura show frequently a further complication by the possession of a suprastapedial element. This I consider as originally not belonging to the interfenestral chain. It is, as, for instance, in *R. pipiens* (fig. 9A), very long, turned back, and attached to the auditory capsule, and has nothing to do with the stylohayl.

Summing-up of the Dipnous and Amphibian Features in comparison with those of the Fishes.—1. The gradual, and lastly absolute, estrangement of the hyomandibular-hyoid arch from the palato-quadrato-mandibular arch, which leads eventually to the loss of ligamentous connexions, and to the final attachment of the hyoid to the cranium.

2. The complete separation of the hyoid from the hyomandibula (analogous to that observed in certain Rays).

3. The same setting free of the hyomandibula, which would have become completely aborted unless it had assumed new—namely, auditory—functions, by becoming connected with a tympanum; *i.e.*, a cavity formed out of the Piscine first visceral cleft.*

4. The breaking up of the hyomandibula into two and more pieces, as an ossicular chain.

5. The loss of the old piscine ligamentous, and sometimes even cartilaginous, connexion between the hyomandibula and the mandible, so that the Amphibia have returned to an absolutely autostylic condition.

6. The gradual loss, in the Urodelous group, of a piece of cartilage (PARKER's hyomandibula of *Menopoma* and *Proteus*), which piece is comparable with either a symplectic or with an opercular element.

7. The connexion of the tympanal end of the auditory chain or rod with the cranium by a suprastapedial element of probably periotic origin.

8. The reduction of the quadrate to a small cartilage, wedged in between the elongated pterygoid and squamosal bones. This elongation of the pterygo-quadrate bar, or the transposition of the masticatory joint far outwards, away from the cranium, has caused, or has at any rate facilitated, the separation of the hyoid from the hyomandibula.

Chelonia (Plate 74).—The broad quadrate is fused with the skull. PETERS has drawn attention to the following difference between the various families. In the Trionychidæ and in the Land Tortoises the quadrate bone forms a closed canal, through which passes the columellar rod. In the other Water Tortoises and in the Turtles, however, the quadrate forms only an imperfect canal, which is open behind and below, rendering the whole columella visible from below

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* HOWES' discovery of a tympanum in *Raja* is most important; it shows, although perhaps by analogy only, how the approach of the hyoid to the cranium is correlated with the change of function of the first cleft.

In all Chelonians the interfenestral apparatus consists of two pieces. A long bony rod, or columella proper, fits into the fenestra ovalis; to its outer end is attached a broadened-out cartilaginous plate, which is firmly attached by connective tissue to the small tympanum. We can scarcely speak of a tympanum proper, because its place is covered over by the ordinary skin of the sides of the head. I found in a half-grown *Chelone imbricata*, after removal of the skin, a small globule of fibrous and partly ossified cartilage, of the size and shape of half a pea. Its convex middle was attached to the columella, and the plane disk fitted exactly and firmly, like a plug, into the small tympanic part of the auditory meatus. There are no special ligaments which connect this plug or the columella with either cranium, quadrate, mandible, or hyoid.

The latter is frequently either absent or is a mere bit of bone or cartilage, attached to the basilingual plate—*e.g.*, in *Emys*. All between this remnant and the cranium has disappeared, not even traces of a stylohyal or craniohyal ligament being left. The pair of long bony bars, which acts as hyoid, is in reality the third visceral or first branchial pair.

Crocodilia.—The auditory apparatus is very complicated. It was first accurately described by PETERS, who discovered and figured the connexion of the outer columellar element with the mandible. The following is a description of the arrangement which I have found in a young *Alligator mississippiensis*, whose skull is 15 cm. in length.

In order to make the preparation which is figured (fig. 14, Plate 72), the bones, after removal of the skin and the masticatory muscles, were gradually filed down in a plane parallel with the long axis of the quadrate bone.

The air cavities of the os articulare of the under jaw stand in connexion with the middle ear or tympanic cavity by the fibrous and partly cartilaginous siphonium. This is situated at the hinder corner of the quadrato-mandibular articulation.

To the same part of the os articulare, immediately behind the siphonium, is attached a cartilaginous and partly ligamentous string, which extends upwards along the hinder surface of the quadrate; this bone forms a slight semi-canal, which in its proximal posterior region becomes a complete wide canal. Through this passes the cartilaginous rod or ligament, and, where it enters the tympanic cavity, it is attached to the cartilaginous lower process of the distal element of the columella. This distal columellar cartilage consists of a short stem, which articulates with the columella proper, and of three irregularly-shaped processes. The lower one is connected with the mandible as described above, the anterior or most lateral one is attached to the middle of the tympanum, whilst the third is fixed on to the hinder upper corner of the tympanum. To the anterior or most lateral (HUXLEY's extrastapedial), not to the "suprastapedial" process, is attached the tendon of a tiny muscle which arises from the anterior cartilaginous brim of the tympanic cavity; it is a m. tensor tympani. The same periotic region is connected by thin ligamentous tracts with the upper, posterior process. The extracolumellar-mandibular connexion is subject to many variations. According to HUXLEY, the cartilage which is attached to the "infrastapedial" process, and which he calls the styloid cartilage, lies in his young *Crocodilus acutus* "upon the upper and posterior face of the quadrate bone; its lower extremity terminates some distance above the upper end of the pneumatic duct, the fibrous wall of which is continuous with the sheath of connective tissue which envelopes the cartilaginous rod in question." This latter tapers below to a free rounded extremity.

PETERS found (1868) in an embryo of the same species of 20·5 cm. in length "a small and short cylindrical cartilaginous piece between the distal end of the columella proper and the trifid malleolar cartilage"; he compares it with either the os lenticulare or with the incus of the Mammalia. In a still younger embryo of *Crocodilus vulgaris* he found the transition of the lower extracolumellar process into MECKEL'S cartilage very plain and obvious. In his paper on the pneumatic duct of Crocodiles (1870) he describes and figures a whole series of modifications of the parts in question. The principal results of his investigation, which also agree with the specimens examined by myself, are the following (see fig. 19, and PARKER'S illustrations, figs. 15–18):—

1. The outer end of the columella proper possesses a concave facet by which it articulates with the short basal stem of the trifid extracolumellar cartilage, or malleus.

2. The lower process of this trifid piece passes into a long cartilage (HUXLEY'S styloid), which is continued into the swollen cartilage of MECKEL at the posterior and upper articular corner of the mandible.

3. The siphonium connects the air cavities of the os articulare directly with the tympanic cavity, but not with the air cavities of the os quadratum, the latter are, however, in direct communication with the tympanic cavity

4. Siphonium and mandibulo-extracolumellar connexion are independent formations, although the fibrocartilaginous siphonium is continued upwards into the connective tissue which partly lines the bony canal of the quadrate, through which passes the mandibulo-extracolumellar string; the siphonium is, therefore, "continuous with the sheath of connective tissue which envelopes the cartilaginous rod in question," as HUXLEY describes it.

5. This whole string is originally entirely cartilaginous. Fig. 19 shows the gradual transformation into connective tissue of the cartilage at the distal end of the lower process of the trifid piece and at the mandibular end; this leads sometimes to the reduction of the cartilaginous rod to a very small cartilage, which remains as a pulley-like arrangement in the region of the complete tympano-quadrate canal. See fig. 14 (*Allig. mississ.*).

6 There is a musculus mallei, *s.* tensor tympani, but not a m. stapedius nor a m. incudis.

The lingual skeletal parts of the Crocodilia are much more reduced in number than those of the Chelonia. There is, besides the broad shield-shaped unpaired basilingual piece, only a pair of thyrohyals or ceratobranchials, which, of course, are homologous with the third pair of visceral arches. The second, or hyoid, pair has entirely disappeared as far as ceratohyal and stylohyal pieces are concerned

It is obvious that the system of cartilages and ligaments extending from the fenestra ovalis to the mandible is at least analogous with the cranio-mandibular or suspensorial connexion, *i.e.*, the hyomandibulo-symplectic elements, of the Fishes

Parker, the latest worker on the Crocodilian ossicular chain, gives in his essay (Plate 68) a series of beautiful figures of embryonic Alligators and Crocodiles (see figs. 15–18), which demonstrate the correctness of Peters's observations and conclusions. Whilst in the earlier stages there is a continuous rod of cartilage passing from the tympanal region down and behind the quadrate into the portio articularis of Meckel's cartilage, this cartilaginous continuation is, in the 5th stage embryos (of 4½ inches total length), near the siphonium, reduced to a ligamentous one Parker (p. 272 and p. 281) compares the mediostapedial shaft of the columella with part of a pharyngohyal element, which is equal to the hyomandibula of Fishes; "the unossified proximal end is always a separate cartilage (stapes) in the Amphibia." All the rest outwards from the lateral end of the columella down to the mandible he compares with the hyoid bar proper. His nomenclature of the whole second visceral arch, as given on p. 272 of his work, and reproduced in fig. 16 of this essay, is this:—

1. Columella = hyomandibula.
2. The "suprastapedial" is a special hyoid element not found in normal branchial arches, and restricted as a separate piece to the Crocodilia.
3. The "epihyal," already ligamentous in later, nearly ripe stages like those of Peters.
4. The main bar or ceratohyal. It "lessens downwards, becoming terete, and is thoroughly fused below with the mandible, close behind the articulation with the quadrate, in embryos of *Alligator mississ.* (of 1½ inch total length). The rest of this arch at present is merely a median hyobranchial tract, the hyoid part of which lies in front of the first ceratobranchials or paired thyrohyals."

Parker assumes consequently the absolute fusion of the distal end of the ceratobranchial with Meckel's cartilage, and the disappearance of the original connexion which must have existed between the ceratohyal and the hypohyal, "which latter is not distinct from the common basi-hyo-branchial plate" (our basilingual cartilage). This view is wrong. We do not know in either Elasmobranchs, Dipnoi, or Amphibia of any ligamentous connexion of the mandible with the distal, or even with the middle, portion of the hyoid bar, but only and occasionally with the proximal end of the hyoid; a ligament which could possibly lead to a cartilaginous junction between hyoid and mandible. On the other hand, the possibility of a cartilaginous connexion between the distal end of the hyomandibula and MECKEL'S cartilage is demonstrated by Elasmobranchs

Hatteria (fig 11).—This very primitive Reptile has been used both by HUXLEY and PETERS to prove their views with regard to the morphological value of the auditory ossicles.

HUXLEY'S description has to be given in full. He says (1869, p. 396):—"Nothing can be more instructive than the arrangements represented in fig. 3. *Sphenodon* has no externally visible tympanic membrane; but on removing the integument which lies over the aural region and the anterior portion of the digastric muscle, the fibres of a strong aponeurotic expansion, which takes its place, are seen to pass from the posterior edge of the quadrate bone and from the angle of the mandible to the anterior margin of the anterior corner of the hyoid, the upper part of which is entirely cartilaginous The hyoidean cartilage ascends behind the quadrate bone, with a slight backward convexity, until it has nearly reached the skull, and then appears to be suddenly bent in the form of a little scroll with a backward concavity. The upper end of the scroll becomes connected with the skull; the concavity is filled up by aponeurotic fibres.

"The aponeurotic expansion which has been mentioned covers the outer end of the tympanic cavity; when it is removed, the proximal end of the corner of the hyoid is seen to expand, and becomes converted into a broad plate of cartilage, the curved margin of which gives rise to the scroll. Internally, the plate is continued into the stem of the stapes, and speedily becomes ossified. There can be no doubt, therefore, that it corresponds with the extrastapedial cartilage of the Crocodile. What answers to the axe-head-shaped suprastapedial cartilage of the Crocodile is the upper process of the cartilaginous part of the stapes, which, however, passes into the extrastapedial cartilage externally and above, so as to enclose the foramen *a*. On the left side, the suprastapedial process was fibrous at the point *b*. Superiorly, the suprastapedial cartilage is directly continued into the cartilaginous termination of the parotic process of the skull, in which granular osseous matter is deposited."

"Thus the suprastapedial cartilage turns out to be nothing more than the proximal end of the hyoidean arch, while the stapes and its appendages are exclusively related to this arch, and have nothing whatever to do with the mandibular arch."

HUXLEY assumes the absolute continuation of the hyoid into the stapes, whilst the proximal end of the hyoid projects on to the parotic cartilage. PETERS (1874) does not deny this ligamentous connexion, nor even the partial coalescence of the hyoid with the malleus, but he looks upon it as secondarily acquired. He observed that "the fibres of the hyoid are softer and have a different direction to those of the harder fibres of the malleus, the two sorts of fibres crossing each other." The swelling of the hyoid, when it is apposed to the extrastapedial cartilage (malleus), does not owe its existence to the cartilage itself, but to connective tissue. Moreover, the hyoid is not connected with the inner or lower process of the malleus, but it passes above it without being attached to it, so that the open space, figured in HUXLEY's and in PETERS's specimens, is not a foramen, formed by junction of the hyoid with the two processes, but is only a notch Undoubtedly, PETERS continues, the mandible was formerly connected with this inner axe-shaped process

The proximal end of the hyoid is connected, as in HUXLEY's specimen, with the cartilaginous parotic styloid process. It is jammed in between the quadrate, parietal, and exoccipital or mastoid bone. This position of the proximal end of the hyoid above, and slightly in front of, the auditory ossicles is satisfactorily explained by PETERS by the peculiarly slight development of the proximal part of the quadrate bone and its firm connexion with the mastoid, so that the latter is removed from its original position.

BAUR mentions only that in three specimens of *Hatteria* the cartilages in question were partly coalesced, but that "series of sections showed that the hyoid arch was free from the malleus proper," and "that these conditions were less clear than he expected"

My own investigations were made on five adult and half adult specimens. The tympanic cavity is represented by a large pharyngeal recessus. The membranous walls of this recessus are attached as follows —The anterior wall lines the whole of the posterior aspect of the broad quadrate, and it closes the space between the inner brim of the quadrate, the pterygoid, and the anterior ventral sharp edge of the exoccipital bone This wall lies consequently in front of the columellar rod. The posterior wall of the recessus is spanned out between the sharp lateral brim of the conjoint exoccipital bone and the basisphenoidal lateral process, thence it extends to the posterior angle of the mandible, and to the posterior inner surface of the hyoid up to the quadrato-exoccipital junction. This wall lies consequently behind the columella. There is no auditory opening visible externally, the outer skin covering the whole region, but underneath the skin we find the space between quadrate, mandible, and hyoid closed by strong fibrous connective tissue, which represents an imperfect tympanum (see fig. of specimens A and B).

Specimen A, apparently adult.—The extracolumellar cartilage has no foramen whatever, nor is it attached to the cranium directly, except by a strong ligament, which arises from the parotic corner and attaches itself to the extracolumellar cartilage on its outer margin, after having passed over the greater part of the cartilage. The more superficial fibres pass on and diverge to the outer brim of the quadrato-mandibular articulation and to the mandible alone. In other words, there is a cranio-quadrato-mandibular ligamentous tract = cranio-extracolumellar + extracolumellar-quadrato-mandibular tract.

There is, further, a thin membrane of thin elastic tissue between the whole lower and anterior convex margin of the extracolumellar cartilage and the quadrate, mandible, and hyoid, as shown in fig. A. This membrane is situated internally to the other tracts.

The long "infrastapedial" process is jointed to the top end of the slender hyoid cartilage. The proximal third of this hyoid is connected with the posterior inner knob of the mandible by sharply-defined tendinous fibres, which gradually form a distinct and strong hyoideo-mandibular ligament.

Specimen B.—The formation of the imperfect tympanum by means of a tendinous fan-shaped connexion between the parotic corner of the cranium and the quadrate, mandible, and hyoid, with the important feature of the extracolumellar cartilage being attached to the middle of this tympanum, shows some modifications (fig. 11). As in specimen A, the extracolumellar cartilage does not touch the cranium, but its "infrastapedial" process passes without a break into the hyoid, and the fibres of the triangular hyoideo-mandibular ligament do not arise from the hyoid alone, but also from the "infrastapedial" process

Specimen C is of the greatest importance. The slender hyoid is continued as a curved "scroll" along the anterior and lower margin of the extracolumellar cartilage upwards to the parotic corner, where it does not fuse with, although it directly touches, the cranial cartilage. Moreover, there is a foramen, although far smaller than that of HUXLEY's and PETERS's specimens, it being of the size of a pin-hole only. This foramen, which is absent in specimens A and B, and the circumstance that in specimen C as well as in HUXLEY's and PETERS's specimens the hyoid is continued up to the cranium, strengthen PETERS's view that this foramen is formed by the hyoid and by the extracolumellar processes. The hyoid is fused with the margin of the extracolumellar cartilage, and causes a thickening of its margin. Stained microscopical sections show this fusion to be a secondary one. The cartilaginous cells of the thick margin run in the same direction as the whole hyoid, whilst those of the extracolumellar plate run at right angles to them; moreover, in another specimen, which likewise possessed the cranio-hyoid connexion, the cells showed the arrangement represented in fig 11 *C.* 1. Similar sections through specimens like A and B show only a uniform arrangement of the cells from the stem of the extracolumellar piece to its margin.

Another important point in specimen C is that the hyoid does not form the continuation of the lower or infrastapedial process itself, but that this latter is free, it being situated somewhat more inwards, as shown in fig. 11 *C.* 2, and from the distal end of it starts the lig. hm. m.

We conclude, therefore—

1. That the fusion of the hyoid with the extracolumellar cartilage is a feature acquired secondarily and owing to juxtaposition.

2. That the proximal end of the hyoid was originally connected with the parotic cartilage of the cranium; and that

3. This contact-connexion disappeared (specimens A, B, D), whilst the hyoid portion from 5 to 4 either remained—be it fused or not fused with the extra columella—or disappeared (specimens A and D).

4. There are occasional traces of a ligamentous connexion between the distal end of the "infrastapedial" process and the mandible, notably in specimen C, besides a hyoideo-mandibular ligament.

Nobody can assume that this hyoideo-mandibular ligament is homologous with a continuation of MECKEL's cartilage into the upper half of the ceratohyal, as PARKER suggested for the Crocodilia. Such an idea is to be discarded because of the entire preservation of the ceratohyal portion in *Hatteria*, and because of the important circumstance that the strong ligament *l.h m e.* is attached to the posterior corner of the mandible, whilst the thin infrastapedial + hyoideo-mandibular tracts are attached to the inner articular knob of the articular part of the mandible

We can recognise in this small inner ligament the last trace, now nearly aborted, of the infrastapedial-mandibular tract of the Crocodiles. Moreover, the Crocodilian "suprastapedial" recognised by PARKER as part of the hyoid is possibly contained in the strong parotic-extracolumellar ligament of *Hatteria*, and it is not beyond the limits of possibility to assume that a Crocodilian free "suprastapedial" of PARKER would result from the reduction of the part *e–i* of the hyoid.

Uromastix spinipes—PETERS found an articulation between the columella and the extracolumellar cartilage; from this latter, near its articulation, descends a process downwards, which changes gradually into a ligamentous or tendinous thread; it descends on the inner side of the quadrate, passes through between the quadrate and the hinder end of the pterygoid bone, and passes lastly into the mandible in front of the inner margin of the articulation with the quadrate. He naturally looks upon this thread as the continuation of the extracolumella into MECKEL's cartilage. The following descriptions refer to my own observations.

Psammosaurus scincus (fig 12).—In this North African Lizard all the points in question are easily examined after the severing of the head from the neck. The whole pharynx and part of the tympanic recessus are pigmented black, except the anterior wall of the recessus and the tympanum itself. The tympanum is complete and visible from without. The long hyoid bars are far removed from the skull. The hinder body of the tympanum itself is formed by a strong yellow tendinous tract, which extends from the outer exoccipital corner to the upturned angle of the mandible. The extracolumellar cartilage articulates with the columella. Its shape and its connexion with the tympanum are best explained by the figures (12). There is a short and strong ligament from the parotic corner to the uppermost short process of the auditory cartilage. As in *Uromastix*, there is a long basal process; it is continued into a round fibrous thread, which squeezes itself in between the quadrate and pterygoid bones. After the end of the pterygoid has been broken off the thread is seen to be attached to the inner side of the distal part of the quadrate, some tendinous fibres being continued towards its distal end, but not to the mandible.

From the mandible, immediately behind its articulation with the quadrate, MECKEL's cartilage is continued upwards as a round string of fibrous tendinous tissue, but this string attaches itself to the exoccipital parotic region, and sends hardly any fibres to the stem of the extracolumella, while it passes to the inside of it.

Hydrosaurus salvator, from Australia, shows the same arrangement as that represented in fig 12.

Teju (fig. 13).—Large specimen of five feet in length. The columella articulates with the extracolumella by a complete joint. A strong yellow tendinous ligament connects the parotic corner, between the exoccipital, squamosal, and quadrate, with the two tympanic processes of the extracolumella, and is then continued as an indistinct ligament to the mandible. The ligamentous thread from the inner lower process is lost between the pterygoid and quadrate bones. There is no extramandibular continuation of MECKEL's cartilage. The hyoid is long, and far removed from the skull.

Gecko mauritanicus, adult (fig. 10) —The long hyoid bar is attached to the cranium by a strong ligament, but there is no connexion whatever of the hyoid with the extracolumellar cartilage. The upper short process of the latter is, as in some other Saurians and in the Crocodiles, connected with the skull by a short "suprastapedial" ligament. Mandibular connexions are absent BAUR makes a statement which I have not been able to corroborate, viz., that the "infrastapedial" process is connected with the mandible by a fine thread. This thread he homologises with the extramandibular part of MECKEL's cartilage. On the other hand, I find PETERS's remark correct (1869, page 6), that a fine semicartilaginous thread from the infrastapedial loses itself between pterygoid and quadrate.

Chamæleo vulgaris (fig. 20).—There is no tympanum. The hyoid is far removed from the skull. The columella is a long, bony, and slender rod, which, according to PARKER ('Chameleon,' p. 96), is already in the young confluent with the oval stapedial plate which fits into the fenestra ovalis: "Where the bone ceases there the extrastapedial region begins; but any segmentation of the cartilage, which may have existed, is gone."

"The extrastapedial cartilage is attached to the inner side of the quadrate behind, in its normal ichthyic condition, for there is no drum cavity in this type, and therefore the extrastapedial does not ride over the edge of the quadrate. There is a fenestra in the proximal part of the cartilage, and above this space the thickened inner edge of the cartilage passes upwards as a short suprastapedial; this is finished above by an enlarging ligament, which is inserted on the inner face of the quadrate, close to the top."

The remarkable points of *Chamæleo* are therefore—first, the apposition and fusion with the inner aspect of the quadrate of those parts of the extracolumella which in other types would be attached to the tympanum; secondly, as a result from this fusion, the absence of an extrastapedial or central tympanal process; thirdly, the absence of a special connexion of the infrastapedial process with MECKEL's cartilage, owing to the fusion of the former with the quadrate. That cartilage which PARKER calls (*cf.* fig 20B) the extrastapedial in *Chamæleo* I homologise with the infrastapedial = long process of the malleus, and assume the reduction of the true extrastapedial. The presence of the little fenestra is the last remnant of the rectangular space or niche between these two processes in other Lizards.

Ophidia, Pelophilus madagascariensis, adult (figs 22, 23, Plate 73).—The columella is entirely bony, and is of nearly the same length as the long horizontally-placed squamosal bone. To the end of the columella is attached a small, peculiarly shaped moveable cartilage; this extracolumella has a concave smooth facet, which freely with a convex smooth facet of the quadrate, as shown in fig 22B, around and articulates between this articulation lies a ring-shaped complete meniscus of hyaline cartilage, one end of this meniscus goes over into connective tissue, which is lost on the periost between the inner corner of the quadrate and pterygoid bones, the other end of the meniscus passes into similar connective tissue, which surrounds the whole columella like a sheath, and attaches itself with tendinous fibres to the cranium below and a little behind the proximal end of the columella. The little extracolumella has no connexion whatever with either the sheath or with any other parts except with the columella itself

Crotalus durissus, adult (fig. 24).—The squamosal bone is very short and weak, the long and slender quadrate having almost entirely replaced it by position and function. The distal end of the pterygoid does not at all touch the quadrate, but is connected with it by a ligament, much longer than that in *Pelophilus.* One pair of hyoid-like, very thin cartilaginous arches runs down the sides of the trachea.

The columella and the extracolumellar cartilage are like those of the Boa. The cartilage articulates upon a sharpish ridge of the quadrate, but there is only half a meniscus on the inner side. The columellar sheath, which is strongest on the posterior and inner side of the bony rod, is continued as tendinous tissue to the fibrous quadrate-pterygoid ligament, and partly towards the end of the quadrate

PARKER gives a description and figures of the embryonic Snakes (fig. 21), which I cannot quite reconcile with his description of the ripe stage. He says (Embryos of 3rd stage), p. 398,—"the hyoid fold has cartilage only in its upper third; this is a rib-like piece, with a rounded capitulum, a solid tuberculum, and a sickle-shaped shaft, whose convexity is backwards. The hind edge below has a crest ready to separate from the main part The capitulum is attached to the membrane of the fenestra ovalis (*st.*), which is beginning to chondrify continuously with the hyoid rib-like rod." On p. 406 (Ripe Embryos) he says: "the backward extension of the huge mandibular arch has thrust it past the hyoid rudiment; this is the cause of the very peculiar position of the stylohyal and columella on the inner face of the quadrate—notwithstanding the small size of the arrested hyoid arch, it has become segmented into two normal pieces; the columella (minus the stapedial plate) answering to the hyomandibula, whilst the stylohyal is the upper part of the familiar 'stylo-ceratohyal' bar. There is no distinct membrana or cavum tympani, and at present the stylohyal cleaves to the columella. This element is reniform (*st. h.*) and its middle and convex portion is covered with a scabrous ectosteal plate; this and the extrastapedial are jammed between the skull and quadrate. The terminal third of the columella is unossified = extrastapedial part, and it has no suprastapedial spur." In a foot-note, PARKER says .—"in every Ophidian skull examined by me there was to be seen a thin scale of bone adherent to or coalesced with the inside of the quadrate, above its middle. The arrested stylohyal is stowed away there, permanently faint and functionless."—"There is no cartilage in the distal part of the Snakes' hyoid or lingual region" (p 407) "Of the hyoid arch remain in the adult only two rudiments; both have lost their independence, the antero-posterior or hyomandibular element is now the small columellar prickle on the oval stapedial plate; the postero-inferior piece is starved and useless, it is anchylosed to the quadrate, towards the back of the upper third (*st. h.*). There is no distal or lingual cartilage" (p. 415).

PARKER's reniform cartilage is the extracolumella of our nomenclature, and not the stylohyal, as PARKER was compelled to assume, since he homologised the terminal unossified third of the columella with the "extrastapedial part" (our extracolumella). The tract of connective tissue which, in his fig of the 3rd stage, is shown to run forwards from his "hy" (my hyomandibula) may well represent the last trace of the aborted hyoid, as would be the case in *Hatteria*, specimen A, if the ceratohyal were no longer cartilaginous but reduced to connective tissue.

It is easy to connect the Ophidian arrangement with that of the Chameleons. Juxtaposition of the extracolumella and the quadrate bone leads to fusion of these two parts, and this dispenses with any extracolumellar-mandibular connexion. The occasional existence in the Lizards of a double connexion of the extracolumella, namely, with the quadrate and with the mandible, indicates that these Reptiles have retained more primitive features than either Chameleons or Snakes. These remind us of other highly specialised types, the Chelonia. These three types have all, although each through different causes, lost the tympanum and the tympanic cavity proper, the extracolumellar-mandibular connexion, and the greater part of the hyoid.

That neither of the extracolumellar connexions can contain ceratohyal elements is proved by the adjoined table, which shows that there is no interdependence between the parts tabulated.

	Extracolumella connected with—		Hyoid long, attached to cranium or to extra-columella.	Hyoid long and free	Hyoid aborted
	Quadrate.	Mandible (MECKEL's cartilage)			
Hatteria	+	+	+	—	—
Hydrosaurus, Psammosaurus, Teju	+	+	0	+	—
Chamæleo	+	0	0	+	—
Ophidia	+	0	0	0	+
Chelonia	+	0	0	—	+
Aves	0	+	In embryo columellar connexion	—	+
Mammalia	0	+	+	—	—
Anura	0	0	+	—	—
Urodela	+	0	—	+	—
Sphyrna	+	+	to hyomandibula	—	—
Oxyrhina	0	+	"	—	—
Torpedo	0	+	"	—	—
Trygon	0	+	to cranium	—	—
Hexanchus	0	0	"	—	—

We have then amongst the Reptiles to look for types which have preserved more primitive conditions if we want to connect the Reptilian auditory ossicles or cartilages with those of the lower and higher classes. Such types are *Hatteria*, the Crocodiles, and most of the Lizards proper. These taken together show the following important features

1. The connexion by tendinous, and partly by cartilaginous, tissue of the extracolumella with the quadrate and with MECKEL's cartilage.

If we put columella + extracolumella = hyomandibula, we recognise the hyomandibular-quadrate ligaments and the cranio-hyomandibulo-mandibular ligaments of Urodela and Pisces.

The apparent absence in the Urodela of a direct hyomandibulo-mandibular connexion is explicable by the disappearance of the loose "symplectic" cartilage. Moreover, in the Urodela both visceral arches are slanting forwards, so that the masticatory joint is placed far forwards from the otic region, and the anterior pterygo-quadrate-mandibular angle is frequently greater than 90°; in the Reptiles the reverse takes place, the angle is by far less than 90°, and its apex is placed in a level below and even far behind the otic region.

2. The existence of a cartilaginous and osseous severally-jointed connexion between the tympanum and the fenestra ovalis, as in Anura, Mammalia, and Aves.

3. The attachment of the proximal end of the hyoid to or near the periotic region of the cranium, as in the Anura, unless the hyoid has become free or has degenerated. For this latter condition we have no analogous cases in the Urodela, because in them the reduction of the hyoid to a slender rod has not yet taken place, nor has the hyoid lost its primitive feature as the distal complement of the whole original second arch.

Aves.—The arrangement of the auditory ossicular apparatus is very similar to that of the Monitors, as is shown in Plate 74 HUXLEY draws attention to the absence of even a rudiment of a styloid cartilage, and to the elastic ligament discovered by PLATNER, which represents the "suprastapedial" cartilage of the Crocodile. A tensor tympani muscle arises from the lower part of the occiput, and is attached partly to the extracolumellar cartilage and partly to the tympanic membrane.

PETERS (1868, p. 597) makes the following correct observation·—In an embryo of *Struthio camelus*, whose head measured 3 cm. in length, the extracolumellar cartilage was continued into a very fine thread, which soon swelled into a thicker string of cartilage, this ran down behind the quadrate and passed into the inner articular knob of the mandible, exactly at the same place where, later on in the adult, is found the pneumatic foramen PETERS mentions the same of the embryo of *Spermestes atricapilla*, a fringilline form

Fig. 25A represents the conditions of the auditory chain in an adult specimen of *Rhea americana*. The preparation and the following up of the cartilaginous, and later on ligamentous, thread from the extracolumella to the inner angle of the mandible is rather difficult. The thread, where it passes over the anterior brim of the tympanic cavity, is overgrown and partly enclosed by bony scales of the alisphenoid. Close to the entrance of the thread into the mandible is a pneumatic foramen (*F.pn.*). The inner and posterior aspect of the stem of the quadrate is partly surrounded by a wing from the alisphenoid and by a similar extension from the zygomatic process of the squamosal.

In the adult bird the whole hyoid bar is absent, with the exception of a small cartilage, which constitutes one-half of the "os entoglossum." In the embryo there are, however, traces of the ceratohyal part, represented by a fine tract of connective tissue, which attaches itself to a process sent down from the distal end of the columella. (See PETERS, 1868, Pl. I., figs 4 and 4*a*, and 1870, p. 18, foot-note, my diagram on Plate 74). This is undoubtedly a secondary connexion, analogous to that in *Hatteria*. What is, perhaps, the greatest resemblance to Teleostean features is thus produced by this hyoidean connexion with a point between the extracolumella = malleus = symplectic and the columella = rest of hyomandibula.

Mammalia.—In the embryo MECKEL's cartilage is continued behind the quadrato-mandibular articulation upwards into the processus longus of the malleus (= proc. gracilis, *s.* pr. Folii). This connexion is soon reduced and disappears; threads of the vanished cartilage can occasionally be traced from the tip of the Folian process into GLASER's fissure. It looks as if the approach of the mandible and of the annulus tympanicus to the squamosal bone had squeezed out and destroyed this connexion.

The ossicles of the ear are usually four in number. The malleus articulates with the incus, and sends a long process (manubrium) to the middle of the tympanum. The stapes becomes perforated near its basis by a branch from the internal carotid artery, as SALENSKY has shown. Between stapes and incus lies the small lenticular element, frequently remaining cartilaginous and imperfectly jointed, occasionally absent, *i e.*, not developed.

The hyoid has no connexion with either mandible, palate, quadrate, or with the ossicular chain, but its upper end is fused with the cranium behind the tympanic ring.

The views which have been advocated concerning the homologies of the Mammalian ossicles of the ear are tabulated below; which of these views we shall have to follow can be settled only by the following considerations.—

TABULAR Arrangement of the Views held concerning the Homologies of the Auditory Ossicles of the Mammalia

	Malleus	Incus	Lenticulare	Stapes.	Quadratum	Columella.
TIEDEMANN. (1810)					Processus zygomaticus of squamosal	Columella = whole ossicular chain of Mammalia.
REICHERT (1837)	Articulare	Quadratum	..	End of hyoid	Incus	Hyoid.
GEGENBAUR	Articulare	Quadratum	Symplectic	Hyomandibula.	Incus	Hyomandibula.
PETERS (1867)	All	developed from	MECKEL'S cartilage		Os tympanicus	
HUXLEY (1867)	Quadratum.	Hyomandibular (Suprastapedial)	Hyomandibular	Hyomandibular.	Malleus	Hyomandibula
PARKER, I.	Quadratum	Hyomandibular (Suprastapedial)	Hyomandibular	Auditory capsule	Malleus	Hyomandibula
„ II	Articulare	Quadrate		Auditory capsule	Incus	
SALENSKY (1880)	MECKEL'S	cartilage	..	Tissue around a ramus arteriæ mandibularis		
FRASER (1882)	End of mandibular cartilage.	Proximal end of hyoid		Periarterial tissue.		
ALBRECHT. (1883)	Hyomandibular	Hyomandibular.	Hyomandibular	Hyomandibular	Forms the processus zygomaticus of the squamosal.	
GRADENIGO. (1887)	MECKEL'S	cartilage.	..	Hyomandibula and periotic cartilage		

The all-important question is that of the homology of the quadrate bone. PETERS was the first to prove that the quadrate bone of the Sauropida has in the Mammalia become the tympanic bone or tympanic ring. This incomplete tympanic ring is situated below, behind, and in front of the tympanum, also in front of the tympanic canal and in front of, and laterally from, the ossicular chain, exactly like the quadrate of the Sauropida. Moreover, PETERS found in embryos of *Halmaturus bennetti*, of 8·5 cm. in length, the following remarkable conditions:—"The anterior part of the tympanic bone grasps round MECKEL'S extramandibular cartilage, and possesses on its lower surface a convexity which articulates with the medial side of the ramus ascendens of the under jaw; it also articulates by a smooth surface with a concave facet of the inward-curved angle of the under jaw. Somewhat older specimens of *Didelphys* showed similar conditions, but the tympanic bone was already separated from this second articulation by a thin layer of connective tissue."

PETERS draws the conclusion that the inner or median process of the mandible, which acts as a temporary articular knob, corresponds with the permanent inner articular process of Birds, and, we can add, of Reptiles and certain Elasmobranchs (see there, and fig. 27 and Plate 74).

In a young *Tachyglossus hystrix* PETERS found : The middle of the tympanic ring touches the pterygoid, and here it has a convexity for the inner articulation with the mandible. The processus longus of the malleus is extraordinarily developed, more than in any other Mammal; later on this process articulates with, and even fuses with, the pretympanic end of the tympanic ring, but there was still a small convex surface on the lower surface of the latter bone which indicated the former articulation with the mandible's inner concave facet. The incus was extremely small, and was first discovered in the Monotremata by FLOWER (fig. 26*i*). It fuses with one end with the malleus, and, later on, comes to be placed against the squamosal bone, near the hinder end of the os jugale. (Anchylosis between malleus and incus likewise occurs occasionally in many Rodentia.—DORAN)

The illustrations (figs. 26–30, Plate 73) taken from specimens in the Cambridge University Collection, show that PETERS's observations are quite correct. The long process of the malleus is extraordinarily developed and ossified in *Echidna* (*Tachyglossus*), but owing to the degenerated condition of the under jaw in the adult it no longer reaches the inner angle of the latter. In a young *Orycteropus* I find the tympanic ring still connected with the squamosal bone, and, moreover, there is at the distal end of the pretympanic portion of this ring a distinct process or knob, which indicates the former articulation with the inner angle of the mandible. In *Phascolomys* the long process of the malleus is very strong, passes through a broad fissure between the tympanic ring and the periotic capsule, and even in the adult skull almost touches the typically developed inner angle of the under jaw.

PETERS draws attention to the fact that the quadrate bone most frequently carries a considerable portion of the tympanum, and invariably so when the quadrate bone is immovably fixed to the skull, as in Chelonia and Crocodilia. We add the hardly less important fact that no animal possesses an os tympanicum besides a distinct quadrate bone.

This statement seems, perhaps, open to doubt, because of the existence of a tympanic ring in the Anura. This necessitates a consideration of the embryonic development of the tympanic ring.

According to BALFOUR ('Comp. Embryol.,' p. 483), "the metapterygoid region of the quadrate (in the Frog) gives rise to a posterior and dorsal process, the end of which is constricted off as the tympanic annulus, whilst the proximal part of the process remains as the otic (metapterygoid) process, articulating with the auditory cartilage."

PARKER ('Mammalia,' 1885), figures and describes the annulus tympanicus of the embryo of *Tatusia* as cartilaginous, with an osseous scale on its outer side. In higher

Mammalia this membrane bone becomes preponderant over the cartilage, and causes the whole or nearly the whole of the "os tympanicum" to be developed as a membrane bone, with little or no cartilaginous basis. This explains FLOWER's remark ('Osteology of Mammalia,' 3rd ed., p. 133), that "the inner part of the bulla in many Mammals is developed in a distinct cartilaginous lamella, interposed between the lower edge of the tympanic ring and the base of the skull" The inner and under surface of the tympanic bone is greatly expanded in Mammalia, and forms the auditory bulla. The usual statement (*e g*, HERTWIG's 'Embryologie,' p 461), that the "os tympanicum" is a membrane bone, is applicable only to the higher Mammalia.

PARKER ('Batrachian Skull,' Part III., 1881) informs us that "the annulus tympanicus is the spiracular cartilage, which may chondrify with the otic process of the quadrate pedicle." See also the remarks on p. 460 of this essay.

We conclude that the os tympanicum of Mammals is equal to the quadrate + annulus tympanicus of the Anura = quadrate proper + its metapterygoid region, or that the metapterygoid process of the Anura = greater part of annulus tympanicus of Mammalia; the quadrate proper of Anura = that part of the annulus tympanicus, which, in the young of *Orycteropus*, Monotremata, and Marsupials, lies between the squamosal and the inner angle of the mandible. If, then, the quadrate has been converted into the Mammalian tympanic ring, the whole retrotympanic arm of the latter must be an outgrowth of that part of the quadrate to which, in Lizards and Snakes, is attached the extracolumellar cartilage. In *Pelophilus* there is already such an analogous, although still rudimentary, process.

The masticatory joint has undergone a complete change within the Amniota. In the Sauropida it is an articulatio quadrato-mandibularis, with an inner and an outer facet, both being concave on the mandible, convex on the quadrate. In the Monotremata there is developed a new articular or ascending process on the outer side of the articular region, by means of which the latter gains a new articulation, viz., with the squamosal, the convexity being carried by the mandible.

This alleviates the burden of the quadrate bone as a suspensorial element; it becomes reduced in bulk and gradually gives up its contact with the mandible; the malleus or outermost part of the extracolumella is attached to the quadrate, analogous to that similar attachment in Snakes and Chameleons.

In the Marsupials, traces only of the old suspensorial function of the quadrate remain; and, lastly, in the Monodelphic Mammals, the quadrate is entirely and solely devoted to the auditory service as principal carrier of the tympanic membrane. The masticatory joint has changed from a quadrato-mandibular into a squamoso-mandibular articulation.

Indications of the lessened importance of the quadrate, which is so powerfully developed in the Fishes and in the Urodela, are met with in the Anura, but there the quadrate is not rendered free, but, through its fusion with the squamosal, assumes conditions which at first sight seem strikingly like those which ALBRECHT assumes to exist in the Mammalia.* The cases are, however, analogous only, like other instances of the occurrence of Anurous features in the Mammalia, *e g.*, the two condyles.

HUXLEY, in starting the view that the quadrate bone of Sauropida is transformed into the Mammalian malleus, logically assumed an articulation of the os articulare mandibulæ with the squamosal. He ignores the continuity of the long process of the malleus with MECKEL's cartilage in the Mammalia, but lays stress upon the "continuity" of the auditory chain with the hyoid in certain Reptiles

GEGENBAUR, and lately also PARKER, looks upon the malleus as the modified os articulare, because of its continuity with MECKEL's cartilage, whilst they homologise the quadrate with the incus. They have therefore to assume that the incudo-malleolar articulation corresponds with the masticatory joint of the other Vertebrata. So far as the necessity of a newly-acquired formation of a mandibulo-squamosal articulation is concerned, these authors are right, and ALBRECHT is wrong, who upholds that the masticatory joint is an articulatio quadrato-articularis in all the Vertebrata. ALBRECHT's great merit is, however, to have shown, by logical considerations, that the quadrate bone cannot in any case have become one of the elements of the inter-fenestral or auditory ossicular chain of the Mammalia. These reasons are:—The spiracle is homologous with the tympanic canal and the Eustachian tube. This canal is the cleft between the first and second visceral arches; it lies, therefore, behind the quadrate and in front of the hyomandibula. The cartilaginous auditory chain in the Anura, Sauropida, and Mammalia connects the same homologous parts, viz., the fenestra ovalis and the tympanum. It is universally admitted that at least the columella is a modification of the hyomandibula; therefore the columella lies behind the palato-quadrate-mandibular bar. The stapes-malleus chain (or columella + extra-columella) is situated behind the canalis tympanicus; the last remnant of the external opening, when not completely closed by the tympanum, is represented in Man by the occasional foramen Rivini. This defect I compare with the slit R in the imperfectly-closed tympanum of *Hatteria* and other Saurians (figs. 11, 12). Embryological development shows that the ossicular chain in Birds is originally placed closely against the hinder wall of the tympanic canal, and that it gradually severs itself from the latter, becomes free, and is then placed inside the tympanic canal. Consequently no pre-tympanic element like the quadrate can form part of the ossicular chain, unless there be an element (incus or malleus) which lies in front of, whilst the rest of the chain is situated behind, the canal But this is not the case, neither in any Reptile nor in any Mammal; in the latter the tympanic ring fulfils the topographic conditions required of a quadrate bone. Lastly, the lower branch of the n. facialis runs behind the spiracular cleft, in Elasmobranchi between the ligamentum cranio-hyomandibulare anterius and the hyomandibula (fig. 3), and behind the external auditory meatus in the Mammalia (see PARKER's fig. of Pig's embryo). The chorda tympani, a distal connexion between the hyoid branch of the facialis and the third branch of the trigeminus, passes behind and above the meatus, and in front of the ossicular chain.

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* ALBRECHT (with DUVERNOY, TIEDEMANN, PLATNER, and KOESTLIN) thinks that the Mammalian quadrate is fused with the squamosal, and is, in fact, the "processus zygomaticus." As proof of this hypothesis, he takes the highly pathological skull of a new-born child, in which the left zygomatic portion is partly separated by a suture from the rest of the squamosal. DUVERNOY mentions the same in a *Hydrochœrus* according to BAUR. The latter found the same on the right side of a still-born Tiger fœtus He refers also to COPE's remark upon the quadrate of the Permian Theromorphic *Clepsydra* ". . , this horizontal ramus of the quadrate is nothing more than the zygomatic process of the squamosal bone of the Mammalia, forming with the malar bone the zygomatic arch." This may well be the case. Something very similar would occur after slight modification of that long horizontal anterior process of the quadrate, which is [illegible] PARKER's fig. (16) of the Crocodile.

But there are other reasons besides why the quadrate can be neither the incus nor the malleus of the Mammalia. Provided the malleus is the modified upper part of MECKEL's cartilage, then the incus cannot be the homologue of the quadrate, because of the impossibility of intercalating the quadrate as an incus into the ossicular chain, as a link between the stapes (hyomandibula) + lenticular (symplectic) and the malleus (os articulare). The Monotreme incus cannot be used as a support of such an hypothesis, because its connexion with the squamosal and its gradual abortion are not primitive features; moreover, this half-suppressed incus, and not the malleus, articulates typically with the stapedial part. PETERS correctly thought it highly improbable that the same element which, in the Monotremes, is reduced to a tiny rudiment, should, in the closely-allied Sauropida, still occur as an enormous bone, viz., as quadrate; this is all the more improbable, since the supposed conversion of the quadrate into the still large tympanic ring is so well supported.

HUXLEY (1863, p 403) gives weighty reasons against this incus = quadrate view, in pleading for the "suprastapedial" part of the Crocodiles as the representative of the Mammalian incus.

The quadrate can likewise not be the Mammalian malleus, because in that case that part which, in Reptiles, Birds, and Anura, touches the tympanum, would have to be withdrawn from the tympanum to make room for the changed quadrate, the latter to be intercalated between the Sauropidan tympanum-bearing cartilage (henceforth to be incus) and the tympanum We know of no intermediate stage which might indicate these enormous changes

Lastly, the os articulare cannot have been converted into the malleus, because the latter is, like all the rest of the auditory chain, developed as cartilage; whilst the os articulare is ectochondral bone, like the other bony parts of the mandible. We shall not consider the enormous changes, wholly unsupported by observation, which would have had to be gone through by the ancestral Mammalia during the conversion of the old articulo-quadrate joint into an articulatio incudo-malleolaris, the loss of the quadrato-squamosal connexion, and the development of a new joint and break between the pars dentalis and the pars articularis of the mandible.

There is, then, nothing left but to assume that the distal part of the hyomandibula, analogous to a symplectic, has been converted into the tympanum-bearing malleus.

The continuity of the long process of the embryonic malleus with MECKEL's cartilage is explained by the conversion of the old lig hyomandibulo-mandibulare into a cartilaginous connexion. That this can take place is indicated by Elasmobranchs. Here ALBRECHT errs. Instead of looking upon this connexion as secondarily acquired, he concludes that the hyomandibula forms the proximal half of the mandibular arch, his "costa mandibularis"; the next arch in front (the first of all) is then the palatoquadrate bar, his "costa palatina"; the original visceral cleft between these two arches is then the mouth + spiracle! His third arch is the hyoid alone ("costa hyoidea"). The second cleft is absent as an open one, although he calls it in his diagram a fissura mandibulo-hyoidea. From this follows that ALBRECHT looks upon the visceral arch arrangement of the Rajidæ as more primitive than that of the Notidanidæ. He reverses one of the most clearly and perfectly preserved series of phylogenetic development, as it has been worked out so admirably by GEGENBAUR in one of his most "Epoche machende Werke," and which I have tried to summarise in the first part of this essay.

We consider it as firmly established that the palato-quadrate bar, together with the mandible, forms the first arch. The discontinuity of cartilage between quadrate and mandible is explained by the extreme phylogenetic age of the joint (in *Heptanchus* the continuity of cartilage is still preserved). If we admit that the malleus is formed out of MECKEL's cartilage, we must admit also that the mandibular arch went through a stage similar to that represented in fig. 28, and that the extracolumellar connexion with the mandible in Reptiles is not homologous with MECKEL's cartilaginous continuation, because the latter must then be an articulo-dental connexion.

SUMMARY.

The phylogenetic development of the first visceral arches shows us some most interesting changes of function, which we can follow upwards from the lowest Selachians to the highest Mammals.

Originally entirely devoted to respiration as gill-bearing structures, the whole hyoidean arch becomes soon a factor in the alimentary system. Its proximal half forms the hinge of the masticatory apparatus; its distal half remains henceforth connected with the process of deglutition. Then this suspensorial arrangement is superseded by a new modification; the hyomandibula is set free and would disappear (it does nearly do so in Dipnoi and certain Urodela) unless it were made use of for a new function. With its having entered the service of the conduction of sound, it has entered upon a new departure, and it is saved from degeneration. The whole system of the one to four elements of the middle ear, which all have the same function as conductors of sound, is to be looked upon as *one* organ of *one* common origin, namely, as a modification of the hyomandibula, the primitive proximal paramere of the second visceral arch.

Successive Modifications of the Mandibular and Hyoidean Visceral Arches.

I. Primitive condition. The palato-quadrate bar alone carries the mandible (Notidanidæ). The second arch is indifferent Hyomandibula and quadrate (the palatine part is an outgrowth) are both attached to the cranium.

II. The hyomandibula gains a fibrocartilaginous connexion with the mandible; the masticating apparatus becomes amphistylic and occasionally hyostylic (Rajidæ, most Selachians.)

The hyoid gains a cranial attachment (many Rajidæ).

III The quadrate, or autostylic suspensorium, becomes preponderant; the hyomandibula is, as in Teleosteans, divided into a proximal and into a distal (symplectic) element. The proximal part is received into a fenestra of the otic capsule, and is converted into a stapes, whilst the distal half either remains (*Proteus, Siren, Menopoma*) or is lost (other Urodela). The whole hyomandibula would have been lost owing to its excalation from suspensorial functions, unless it had entered the auditory service.

IV. The autostylic arrangement prevails. The whole hyomandibula remains, gains an attachment on the "tympanum," and differentiates itself into several conjointed pieces, notably stapes, or columella proper, and extracolumella, or malleus.

The extracolumella gains connexion with the parotic cartilage, this connexion frequently remains, but in Anura alone it contains a special element of probably parotic origin.

The quadrate forms an important part of the tympanic frame.

IV.*a*. Collateral departure of the Anura. The connexion between the tympanal part of the hyomandibula with the mandible is lost.

V. The quadrate still forms the principal suspensorial part of the mandible. The extracolumella, or malleus, retains for a long time its previously-acquired connexion with MECKEL's cartilage (Amniota).

V.*a*. The top end of the hyoid is attached to the cranium (*Gecko*, Mammalia), and is occasionally fused with the extracolumella (*Hatteria*).

V *b*. Or the proximal portion of the hyoid is removed from the skull, and remains otherwise well developed (most Lizards), or its proximal portion becomes reduced and lost (Chelonia, Crocodilia, Ophidia, Aves).

V.*c*. The extracolumella gains an attachment to the quadrate, squamosal, or pterygoid, whilst its connexion with the mandible and the tympanum is lost (Ophidia, *Chamæleo*).

VI. The quadrate gradually loses its articulation with the mandible; the latter gains a new, outer, articulation with the squamosal; the quadrate acts entirely as a tympanic frame Incus and malleus fuse sometimes with each other, and lean on to the parotic region. The masticating joint is doubly concavo-convex (Monotremata).

VII. The quadrate is converted into the principal part of the tympanic frame, viz., annulus tympanicus. The mandible has lost its articulation with the quadrate, and the masticatory joint is a single concave-convex one, the convexity belonging to the mandible (Monodelphia).

MODIFICATIONS OF THE VISCERAL ARCHES.

	Amphibia	Reptilia	Aves.	Mammalia.
Ist arch Palato-	quadrato-mandibul	ar arch		
IInd arch				
a Hyomandibula	Forms the cartila	ginous or osseous	apparatus of the	middle ear. [minus
b Hyoid	Principal, hyoid arch	Small, anterior horn	Os entoglossum	Anterior horn, *s* cornu $= \left.\begin{array}{l}\text{cerato} +\\ \text{epi} +\\ \text{stylo} -\end{array}\right\}$ hyal
IIIrd arch (2nd branchial)	Remains in the adult Frog as the cornu thyroideum	Big, second horn	One only well developed horn, wrongly called "hyoid"	Thyrohyal *s* cornu posterius *s*, cornu majus
IVth arch (2nd branchial)		Often big, *e.g.*, in Chelonia	Disap	peared
V. VI VII Pre	sent in Tadpoles, p	artly permanent in	Perennibranchiata	
VIII Present on	ly in Heptanchus.			
Copula between II and III forms the .	} Basihyal, *s.* cor	pus linguæ	Basihyal, *s.* corpus	linguæ.
Copula between III and IV forms the			Urohyal	

EXPLANATION OF PLATES.

The following abbreviations have been used throughout the figures

Als.	Alisphenoid.
asc.p.	Ascending process of quadrate.
A.ty.	Annulus tympanicus, or tympanic bone.
Art.	Os articulare mandibulæ.
Br.I.	First branchial (= 3rd visceral) arch
Cd.	Condyle of occiput.
Cd.m.	Condyle of mandible of Mammalia.
Col.	Columella auris.
C.br.	Ceratobranchial (of 3rd visceral arch).
ep.	Epiotic bone or cartilage.
[illegible]	Exoccipital bone.
[illegible]	Extracolumella = extrastapedial + infra + suprastapedial of HUXLEY and PARKER.
e.st.	Extrastapedial process of HUXLEY and PARKER = manubrium of malleus.

e hy.	Epihyal of Parker.
F.	Fenestra in extracolumella of *Hatteria* and *Chamæleo.*
Gl.	Glenoid facet of squamosal.
l.h.m.m.	Ligamentum hyoideo-mandibulare mediale.
l.h.m.l i.	,, ,, ,, laterale inferius.
l.h.m.l.s.	,, ,, ,, ,, superius
l.hm.m.	,, hyomandibulo-mandibulare
l.hm.q.	,, hyomandibulo-quadratum.
l.hm.h.p.	,, hyomandibulo-hyoideum posterius.
l.m h.i.	,, mandibulo-hyoideum internum.
l.q.m.i.	,, quadrato-mandibulare internum.
Hm.	Hyomandibula = proximal part or paramere of 2nd or hyoid arch.
Hy.	Hyoid or hyoid bar = distal ,, ,, ,, ,,
I.A.	Inner angle of mandible.
i.st.	Infrastapedial process of Huxley and Parker, frequently connected with Meckel's cartilage.
Md.	Mandible.
men.	Cartilaginous meniscus.
m.st	Mesostapedial of Parker = principal part of columellar rod = stem of stapes.
Mk.	Meckel's cartilage.
Par.	Parotic corner of cranium.
Per.	Periotic region.
Pt.	Pterygoid.
p.gl.	Postglenoid process of squamosal.
Q.	Quadrate bone or cartilage.
Sq.	Squamosal.
st.	Stapes.
s.st	Suprastapedial of Huxley and Parker.
Sp.c.	Spiracular cartilage.
Siph.	Siphonium of Crocodilia.
st. h.	Stylohyal = epihyal of Parker = proximal part of hyoid bar

PLATE 71.

Fig. 1A. *Heptanchus cinereus.* Mandibular and hyoid arch ; left, inner view.

Fig. 1B. *Heptanchus cinereus.* Quadrato-mandibular articulation ; left, posterior view.

* The cartilaginous connexion, unaffected by the joint.

L Br I. Ligaments to cerato- and epi-branchial.

Fig. 2A. *Centrophorus granulosus.* Embryo. Inner view of left mandibular and hyoid arches.

Fig. 2B. *Centrophorus granulosus.* Embryo. Outer view of left mandibular and hyoid arches.

l.i = ligamentum intermedium.

Fig. 3. *Oxyrhina gomphodon* Left side, outer view of mandibular, posterior view of hyoidean and anterior view of first branchial arch.

Fig. 4. *Sphyrna zygæna.* Right side, inner view, first branchial arch turned over.

Fig. 5. *Trygon* Cranium with first and second visceral arches; outer view

Fig. 6. *Torpedo marmorata.* First and second visceral arch; outer view

Fig. 7. *Menobranchus lateralis.*

Fig. 8. *Proteus anguineus.* Diagrammatic, after W. K. PARKER

Fig. 9A. *Rana pipiens.* Tadpole. Lateral view of auditory chain; part of tympanic ring cut away. After PARKER.

Fig. 9B. *Otilophus margaritifer.* Half adult. Posterior view. After PARKER.

PLATE 72.

Fig. 10. *Gecko mauritanicus.* Ventral view of left side; hyoid apparatus turned back.

Fig. 11. *Hatteria punctata.* All the figures refer to the left side and are somewhat enlarged, except *C.* 2, which is natural size, and represents the columella and hyoid as seen from the median side.

Specimen *D* represents a posterior view.

Fig 12. *Psammodromus scincus.* Left ossicular chain; natural size and enlarged.

Fig. 13. *Teju* sp. Left ossicular chain, posterior view, enlarged; and right ossicular chain, natural size. *Par.* and *Md.* Attachment of the strong ligament which borders the tympanum, to the parotic corner and to the mandible.

Fig. 14. *Alligator mississippiensis.* Natural size.

Fig. 15. *Crocodilus palustris.* Embryo of 4th stage (3½ inches long). Obliquely external view.

Fig. 16. *Crocodilus palustris.* Embryo of PARKER's 3rd stage (nearly 2 inches in length); lateral view of right side. Nos. 15–18. After PARKER, with his denomination of the parts.

Fig. 17. *Alligator mississippiensis.* Embryo of 5th stage (4½ inches long). Inner view.

Fig. 18. *Crocodilus palustris.* Embryo of 5th stage; outer view of whole hyoidean arch.

Fig. 19 Three stages, to show the reduction of the cartilage between the extracolumella and the mandible; embryos of *Crocodilus palustris* and *Alligator mississippiensis*, 5, 3, and 1½ times enlarged After PETERS.

Fig. 20. *Chamæleo vulgaris.* Posterior views, enlarged, to show attachment of extracolumella to quadrate. After PARKER.

PLATE 73

Fig. 21. *Tropidonotus natrix.* Embryo A. PARKER'S 3rd stage } After PARKER
B. „ 4th „ }

Fig 22A. *Pelophilus madagascariensis.* Inner view of quadrato-mandibular region of the right side, with the muscles, and the extracolumella attached to the quadrate *in situ* Natural size.

Fig 22B. *Pelophilus madagascariensis.* Columella with its sheath and with the meniscus between the extracolumella and the quadrate.

Fig. 23. *Eunectes murinus.* Ventral view, right side. The cartilaginous extracolumella between columella and quadrate is taken away. Natural size.

Fig. 24. *Crotalus durissus.* Inner view of right pterygoid, quadrate, and columella with its sheath.

Fig. 25A. *Rhea americana.* Ventral view. Natural size.

Fig. 25B. *Rhea americana.* Dorsal view of articular region of left mandible

1. Flat articular facet for inner articular process, or distal end, of quadrate.
2. Flat articular facet for lateral aspect of inner articular process of quadrate.
3. Concave articular facet for posterior outer process of quadrate.
4. „ „ „ quadrato-jugal process of quadrate.

Fig. 26. *Echidna setosa.* Natural size.

Fig. 27. *Echidna bruijni.* Natural size.

Fig. 28. *Orycteropus capensis.* Fœtus. Ventral view Natural size. The tympanic ring is still connected with the squamosal. *a.m.* = remnant of the lost articulation with the (lost) inner angle of the mandible.

Fig. 29. *Thylacinus.* Juv. Natural size.

Fig. 30. *Phascolomys wombat.* Natural size.

PLATE 74.

The figures on Plate 74 represent diagrammatically some of the most important modifications of the first and second visceral arches.

XVIII. *Researches on the Structure, Organization, and Classification of the Fossil Reptilia.—V. On Associated Bones of a Small Anomodont Reptile,* Keirognathus cordylus (Seeley), *showing the Relative Dimensions of the Anterior Parts of the Skeleton, and Structure of the Fore-limb and Shoulder Girdle.*

By H. G. Seeley, *F.R.S., Professor of Geography in King's College, London.*

Received April 5,—Read April 26, 1888

[Plates 75, 76.]

The Dicynodont remains hitherto described are nearly all isolated portions of different skeletons, which give no definite idea of the form of body or proportions of the limbs of the animals comprised in the group. The skulls described have been separated from the vertebræ; there has been an absence of matrix to connect either with the limb bones or the shoulder girdle, and, though the pelvis has been found associated with the sacrum, there is no means of judging of its relative size as compared with the head or limbs. Although the Anomodontia are among the most interesting of Reptiles in osteological structure, knowledge of the individual animals is indefinite, and no restoration of the skeleton has been possible.

There is one specimen (Plate 75), however, in the British Museum which contributes materially towards the desired knowledge. It is a small slab of grey-green calcareous shale, numbered 49,413, collected by Mr. Thomas Bain at Klipfontein, Fraserberg, and placed in the National Collection in May, 1878. It is in the worst possible preservation, owing to fracture through the remains, and absence of the counterpart slab, but exhibits the skull, a few vertebræ, ribs, the shoulder girdle, and bones of the fore-limb of a small species of a genus closely allied to *Dicynodon.* The limbs prove to have been unexpectedly short, and, notwithstanding the Mammalian form of pelvis, in other specimens referred to the genus *Dicynodon,* justify the inference that the proportions of the body were rather those of a short-tailed Salamander or Seal than of a Dinosaur or long-limbed Mammal.

The Head.

The skull is exposed in side view with the lower jaw in contact. The extreme antero-posterior length of the head is 10 centims., but this extent is due to the posterior lateral expansion of the squamosal bones at the back of the head, for the measurement from the occipital condyle to the extremity of the snout is 8·5 centims. The vertical measurement from the condyle of the quadrate bone to the summit of the skull is 6 centims., and it is 7 centims. from the infra-articular angle of the lower jaw The lateral contour of the skull closely approaches that of *Dicynodon feliceps*, but that species has the squamosal bone longer, the lower jaw deeper, the maxillary tooth larger, and the back of the head apparently less elevated. *Dicynodon dubius* has the tooth as small as in this specimen, but its root enlarges in the skull, in a way to which this species shows no approximation. Only in *Dicynodon recurvidens* is so small a tooth found as appears to characterize this fossil; but the skull of that species has little in common with these remains. Hence I conclude that the head upon the slab belongs to an undescribed species, with the facial contour of *D. feliceps;* a short vertical quadrate region, as in *D. dubius;* and small teeth, like those of *D. recurvidens*, which, however, were directed downward and forward instead of downward and backward. The scapula shows it to be related to *Kistecephalus;* but the humerus distinguishes it from other genera.

From the back of the head the contour line steadily descends as it extends forward, till over the anterior border of the narine the descent to the alveolar margin becomes rapid. The shape and size of the narine are badly indicated, but its dimensions as preserved are about 17 millims. long by 13 millims. high; hence, the form of the aperture was probably transversely ovate, and its size smaller than the present fractured limits of its margin. It approached near to the roof of the snout, and its superior margin was about 23 millims. above the margin of the jaw, at the point where the tooth crosses it. The orbit appears to have been relatively small, less than 1·5 centim. in diameter. It is separated from the narine by a bar which is less wide than the narine, and is undefined posteriorly, since the post-orbital bar is broken away, leaving a long transversely ovate vacuity, which extends over the temporal region, and measures about 4·5 centims. long by 2·7 centims. deep.

The alveolar margin of the jaw forms a sigmoid curve, being concave from the quadrate bone forward, then convex, with the convexity terminating behind the extremity of the jaw. The small tooth, of which only a fragment is preserved *in situ*, is in advance of the middle of the convexity at 2·5 centims. behind the imperfect anterior extremity of the jaw. By the side of the anterior extremity of the lower jaw is what I take to be an impression of a tooth, which is 3 millims. wide and 17 millims. long. The tooth itself may have been longer and wider. These remains may be parts of the same tooth, with a crown fully 2 centims long, they give no evidence of expansion of the root to a wide pulp cavity, as in *Dicynodon*.

The vertical depth of the head between the orbit and narine is about 4 centims. in the anterior convex part of the alveolar border; and the depth is about the same in the middle of the posterior concave part of the border. This curved outline of the border of the jaw probably results from the breaking away of the maxillary bone, for the pterygoid bone is exposed posteriorly, and is seen to extend downward and unite with the quadrate. The quadrate bone is vertical, and the depth of the skull at the quadrate articulation is 6 centims. This bone is short, as in the true Dicynodons, but not so short as in the Oudenodons. A canal in the sphenoidal region, such as the cochlea might be, is shown in section to be four-sided, with the angles prolonged so as to make its sides concave, and situate far above the upper extremity of the quadrate bone. The lateral expansion and divergence of the squamosal bones outward and backward forms a concavity at the back of the head.

The anterior end of the snout appears to have been rounded and steeply inclined, with an inflation at the anterior corner of the narine; so that the lateral contour of the head approximates to that of the common Turtle.

The lower jaw is 7·5 centims. long. It is short and moderately deep, and terminates anteriorly in a sharp beak, below which the bone retreats in the oblique manner common to Chelonians. The superior and inferior borders are sub-parallel for three-fifths of their length, gently convex above and concave below, with a depth of 1 9 centim., and then its hinder extremity bends downward to the articulation; but the superior border descends more rapidly than the inferior border, so that the vertical measurement narrows posteriorly, and at the articulation the vertical measurement is only 7 millims The articular bone extends obliquely downward and backward, but the extension of the jaw behind this bone is slight.

The preservation of the remains does not warrant a detailed description of the head, and those features which are of interest in it will be better elucidated in remains of other Anomodonts.

The Shoulder Girdle.

The scapular arch of this Dicynodont proves to be made up of many elements. Sir RICHARD OWEN found the scapula and clavicle in the allied genus *Kistecephalus*;* and in another specimen, which was classed as "Dicynodont,"† the scapula is shown to unite with the coracoid and pre-coracoid. The present specimen adds to these elements a very large inter-clavicle and a sternum; and shows the relations of the bones to each other. The preservation of the bones, however, leaves much to be desired, and I offer the following description and restoration with diffidence, which the imperfect condition of the bones may justify, but with some confirmatory evidence from other remains in the British Museum.

The Scapula.

The scapula is formed on the plan of the scapula of *Kistecephalus* (British Museum, No. 17,071), which it closely resembles in form. It has an elongated blade, a distinct acromion, and a transverse articulation, not much expanded, for the head of the humerus. It is badly preserved, and at the proximal end is only indicated by an impression from which the bone is lost, while its free end is imperfect. Its length, as preserved, is 4·5 centims. It is thin throughout the length, which is somewhat curved, is 7 millims. wide towards the distal end, and contracts apparently to about half this width in the middle of the shaft. The anterior border is the more concave, because the bone widens proximally towards the acromion process, which is short, blunt, and directed proximally, as in *Kistecephalus* It widens the bone to 7 millims. Below the acromion the bone is necessarily constricted, or rather notched out, on the anterior side, so that the transverse measurement is 4 millims. And then the proximal end widens to 8 millims at the articulation, and the bone increases in thickness so as to form a flattened articular surface with a sharp margin. The elongated bladelike extension of the bone gives it almost an Avian character; but the acromion process makes it more like the scapula of an Iguanodont. There are no Lizards in which the scapula is similarly elongated and expanded. The Chameleon makes, perhaps, the nearest approximation in relative length, but has not the same distal expansion, nor has it an acromion process The scapula of *Hatteria* is compressed, but it is short, and is differently connected with the coracoid, as though it were connate with the pre-coracoid. It has a slight tubercle on the anterior margin representing the acromion. In Ornithischia the scapula is relatively longer than in *Hatteria*, but has not the expanded form of the free end seen in the fossil, though the acromion may be well marked.* The differences from Ornithosaurs are of a similar nature. The scapula in *Ornithorhynchus* is wider, and relatively less elongated, but resembles the fossil in the articular end, in the supra-articular emargination, and in the extent and direction of the acromion process, which characters may be regarded as Mammalian.

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* 'Catalogue of the Fossil Reptilia of South Africa,' Plate 69, fig. 8, p 63.

† *Loc cit.*, Plate 69, figs. 5, 6, p. 55.

The Coracoid and Pre-coracoid.

Both coracoid and pre-coracoid are developed as moderately large elements in the shoulder girdle, but are represented in the slab by faint impressions, with scarcely a trace of bony tissue. The pre-coracoid appears to have been excluded from the humeral articulation, and to have extended between the scapula and the inter-clavicle. The impression indicates that it may have extended as far forward as the acromial process of the scapula. Its internal border was convex, corresponding with the concavity of the anterior lateral part of the inter-clavicle. Its anterior border is badly defined externally towards the scapula. The extreme transverse width over this pre-coracoid area, below the acromion, is about 1·8 centim.; its antero-posterior extent is about 1·2 centim. There is a small oblong ossification on its anterior border, which is more likely to be part of the expanded plate of the pre-coracoid than part of the clavicle, if the condition of the clavicle in this specimen may be inferred from that in *Kistecephalus*,* in which the scapula is similar. A narrow space, about 2 millims wide, separates the pre-coracoid from the inter-clavicle, and may indicate an unossified band of the pre-coracoid cartilage, but is a defined separation between these sternal elements

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* Scapula of *Crataeomus*, "Reptile Fauna of the Gosau Formation," 'Geol. Soc Quart Journ.,' vol. 37, 1881, p. 656.

The coracoid has its chief extent in the antero-posterior direction. It is overlapped posteriorly by the sternum; and the head of the displaced humerus appears to abut against its lateral border. It contributes almost equally with the scapula to form the glenoid cavity for the head of the humerus. Its surface is smooth. The internal border abuts against the inter-clavicle; and the anterior border, which is straight and transverse, meets the pre-coracoid by a transverse suture which extends into the middle of the glenoid cavity, just meeting the anterior margin of the articular border of the scapula. The bone is vertically oblong, and measures 17 millims in the antero-posterior direction to the border overlapped by the sternum, while transversely its measurement exceeds 1 centim It contributes 6 millims. to the articular cup for the humerus. Its external lateral border below the articulation is concave; and the posterior border is unknown, but probably curves convexly towards the sternum and inter-clavicle. Where the internal lateral border of the coracoid and pre-coracoid meet there is a concavity, which fits against a corresponding convexity of the inter-clavicle.

In *Salamandra maculosa* Professor W. K. PARKER, F.R.S., has shown† that when the animal is nearly adult both coracoid and pre-coracoid elements of the shoulder girdle are present, in addition to the scapula, but neither scapula nor pre-coracoid appears to reach the glenoid cavity, which is formed by the coracoid; and, as no inter-clavicle is present, the type obviously has no near relation to the fossil. The absence of an inter-clavicle is one of the more singular characteristics of the living Amphibia. I am not aware that the pre-coracoid is ever ossified separately in the Lacertilia. The cartilage which is so named never occupies the position, anterior to the coracoid and posterior to the transverse bar of the inter-clavicle, which the pre-coracoid has in this genus. The nearest approach to the condition seen in the fossil is found in the Monotreme Mammals, where a pre-coracoid extends anterior to the coracoid, but it does not unite with the scapula, and extends behind the inter-clavicle, instead of meeting its lateral margin. If the coracoid and pre-coracoid were united, the bone would resemble the coracoid of an Ornithischian The coracoid approximates to the bone in a Monotreme, and in a less degree to *Hatteria*.

Sir RICHARD OWEN has figured‡ a remarkable fragment, which is described as parts of the mutilated scapular arch of a small Dicynodont, which may possibly belong to the same genus as the specimen now described, and indicates an animal with a skull probably about a foot long, if its proportions were those of this species. The acromion of the scapula appears to me to be lost with the fracture (fig. 1) which has removed the greater part of the bone, and the anterior margin of the pre-coracoid is also imperfect, but, otherwise, it affords, when turned round into its natural position, a remarkable confirmation of the natural association of the bones now described. Not the least curious coincidence in structure is furnished by the lateral concavity where the coracoid and pre-coracoid meet on the internal border, showing that the inter-clavicle in that species also had a convexity on the side of the median bar, like that which has been described in this species.

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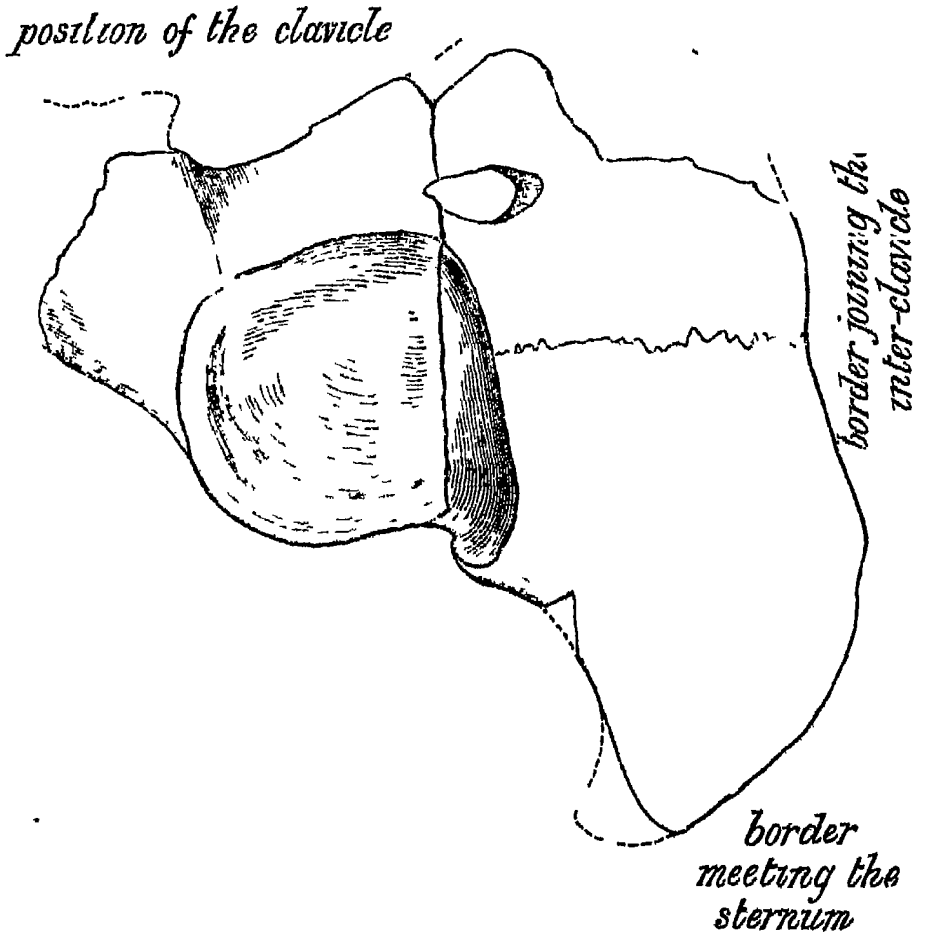
* The bone which Sir R OWEN describes and figures as episternum in *Kistecephalus* ('Cat Rept. South Afric.' Plate 69, p 63) I regard as being the clavicle

† Ray Society, 'Shoulder Girdle,' p. 65, Plate 4, fig 7.

‡ 'Cat Rept South Afric.,' Plate 69, figs 5, 6

Fig 1.



No. 36,287,
Brit. Museum.

The Clavicle.

The clavicle extended along the anterior edge of the scapula as a narrow straight bar running from the acromion to the extremity of the bone. At the acromion it probably made an angular bend, so as to extend along the pre-coracoid to the horn of the inter-clavicle, conforming to the plan of the bone in *Kistecephalus.*[*]

The Inter-clavicle.

The inter-clavicle, if I am right in thus determining the bone, differs from this element of the skeleton in every vertebrate type, apparently in being placed not in

[*] 'Cat. Rept. South Afric.,' Plate 69, fig. 8, *b*, *h*.

front of the coracoids so as to overlap them, but so that they meet its lateral margins. I do not think there is any probability of error in observation on this point, though the bones are badly preserved and only seen on one side of the body The bone occupies the position of a sternum, but I regard it as the inter-clavicle because its posterior end lies in front of a sternum, because its form is that of the inter-clavicle, and because this interpretation harmonizes with the general construction of the remainder of the shoulder girdle.

It is placed like the inter-clavicle in *Iguana*, *Psammosaurus*, and *Stellio*, and is a modification of the T-shaped form seen in those Lizards, in *Ichthyosaurus*, and *Ornithorhynchus;* but it is fundamentally different in form, proportions, and osteological relations from the inter-clavicle of the Pareiasauria. As preserved, it is 3 7 centims. long, is wide, with sinuous lateral margins, and transversely truncated anteriorly, where it terminates in a straight border, 1·8 centim. wide. The two sides are not quite symmetrical, owing apparently to fracture. Behind the anterior border the bone contracts with concave lateral curves, so as to define the cross-bar of the T. This reduces the transverse width to half a centimetre, and there is then a transverse expansion, with convex lateral borders, widening the vertical staff to nearly a centimetre in the anterior half of its length. Then the sides slowly converge, being almost parallel as far as the middle of the sternum, but there are some evidences of irregular transverse expansions near the distal end. The convex expansion in the middle of the vertical staff apparently marks the transverse division between the coracoid and pre-coracoid. The bone is flat, thin, perfectly smooth on its ventral aspect, which is exposed, and apparently lies in one plane

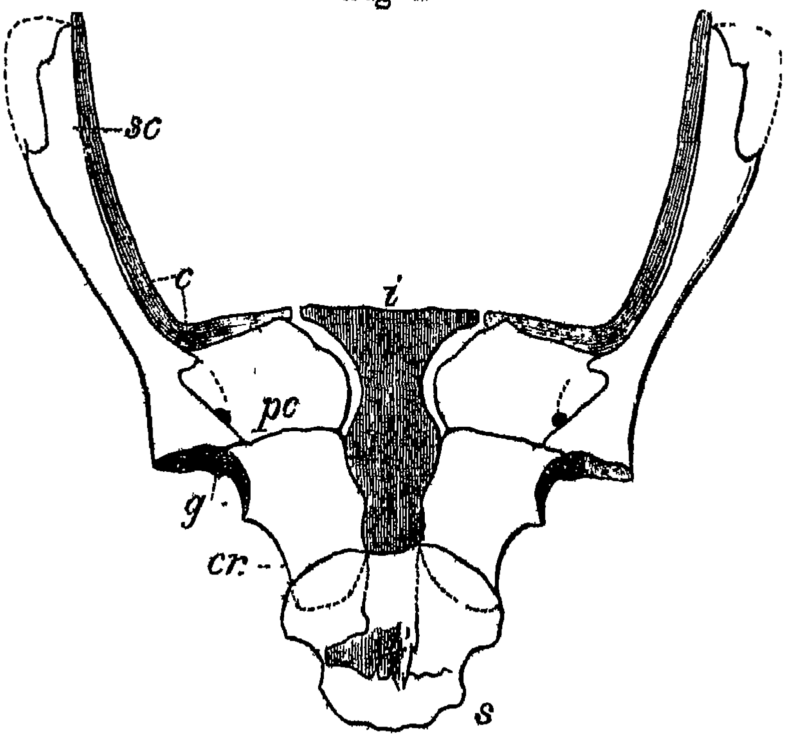
Its wide staff is its most distinctive character, by which it is distinguished from the inter-clavicle of Lizards In *Stellio* the bone is relatively short, but perhaps makes as near an approach to it in plan as is to be found in the Lacertilia. The inter-clavicle of Chelonians does not admit of comparison, because its relations with the pre-coracoid and coracoid are not quite the same. In no Amphibian is there any comparable condition of the inter-clavicle; but in Monotreme Mammals the bone, though relatively shorter in the longitudinal staff, has similar relations to the coracoid, pre-coracoid, and sternum, though in both *Ornithorhynchus* and *Echidna* the anterior element in the sternum is very small. A somewhat intermediate condition is found in the Permian genus *Stereorachis* of GAUDRY.

The Sternum.

The sternum is badly preserved, but its imperfection displays the inter-clavicle extending in front of it almost to its posterior border, though there is some reason for suspecting that the sternum may have been displaced a little forward so as to underlap the posterior borders of the coracoids.

The bone is a thin transversely ovate subhexagonal plate, which is 2·3 centims. wide anteriorly, and 1·7 centim. long, There is no definite boundary between the sides, which all merge into each other by convexities, which correspond with the angles of a hexagon. The anterior border is slightly concave, and about 1 3 centim. long. The antero-lateral borders are about 1 centim. long, and slightly convex. I think it probable that they may have given attachment to the coracoids, since those bones are thus articulated in Lizards and Monotreme Mammals. The posterior-lateral outlines are concave, and more than a centimetre long, and the posterior transverse outline is of similar length, rather convex, and irregular. Only the internal aspect of the bone is seen; its transverse width exceeds the measurement over the distal ends of the coracoids. There is no certain evidence of attachment of ribs to the posterior sternal border, as among Lizards, and they were not articulated to the posterior-lateral border, as in *Hatteria.* Its general form, however, is Lacertilian; and in some Lizards, like *Hemidactylus*, there is a slight posterior-lateral emargination of the bone, which is more marked in *Chamæleo.* In *Ornithorhynchus* the sternum is formed on the typical Mammalian plan, and is, therefore, not comparable with the fossil, and its anterior cartilage with which the coracoids articulate is so small as to be entirely hidden behind the inter-clavicle. The only fossil which it at all resembles is the sternum of *Cetiosaurus*, figured by Professor PHILLIPS,* which he regarded as a transversely ovate bone.

Fig 2



Restoration of the shoulder girdle, natural size.
i., inter-clavicle; *i'*, inter-clavicle seen through a break in the sternum; *s*, sternum; *sc.*, scapula; *c.*, clavicle; *pc.*, pre-coracoid; *cr.*, coracoid; *g.*, glenoid cavity.

The points on which there is some deficiency of evidence in this restoration (fig. 2) are; first, as to the form of the clavicles; fragments of them are found along the whole of the anterior border of the scapula, they are present in *Kistecephalus*, which is nearly allied to this type of Dicynodont, and on the basis of their form in that genus

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* [illegible] 'Geology of Oxford,' 1871, p. 268

I have introduced the bones as having an L-shape, with one limb resting on the scapula, and the other extending transversely in front of the pre-coracoid to the angles of the transverse border of the inter-clavicle. Secondly, it is possible that there may be a foramen on the anterior border of the pre-coracoid; but I attach no importance to the indication, because the character is absent from the other specimens. Thirdly, the sternum may have been a little more posterior in position. I have made the restoration by drawing one side of the girdle from the specimen, and then repeating it on the other side, to make the structure symmetrical

From the description, it is evident that this shoulder girdle belongs to an ordinal type, which is distinct from all known animals. It is intermediate in many respects between *Ichthyosaurus* and *Ornithorhynchus*, but differs from both groups in the presence or relations of the pre-coracoids, sternum, and inter-clavicle. The Ichthyosaurs have neither pre-coracoid nor sternum, and the inter-clavicle overlaps the median union of the coracoids. In the Monotremes the pre-coracoids and coracoids extend behind the inter-clavicle, instead of meeting its lateral borders; but that may be a difference of degree rather than of plan, so that the arrangement in this, as in other respects, comes nearer to *Ornithorhynchus* than to *Ichthyosaurus*. The elongation of the inter-clavicle and size of the sternum are Lacertilian characters, and in Lizards the pre-coracoid element of cartilage does not extend behind the inter-clavicle so that the right and left elements overlap, as among Urodeles and Monotremes Hence from such a type, the Lacertilian shoulder girdle may be derived by loss of the individuality of the pre-coracoid, while that of the Monotreme would result from transverse expansion of the pre-coracoid, shortening of the inter-clavicle, and reduced size of the sternum. On the whole, the Monotreme characters in this shoulder girdle may be regarded as the more remarkable, but they are blended with Lacertilian characters. I do not, however, think that the latter features are approximations to Lizards, so much as a generalized Reptilian inheritance which suggests the Lizard type; and that, on the whole, the Chelonian shoulder girdle may be nearer to Anomodonts than the Lizard's. For the Chelonian stock, before it developed a plastron and lost the separation of the pre-coracoid from the scapula, may well have developed a shoulder girdle in substantial harmony with that which is here restored.

The Humerus.

The humerus is 4·3 centims. long. It is exposed so as to show the width of the proximal end, with the size, form, and position of its radial crest; while distally it shows the transverse thickness of the shaft.

The distal extremity has the articular surface moderately convex from back to front, where the thickness of the bone is about half a centimetre. A little above the articular extremity the shaft contracts somewhat, so as to give a rounded aspect to both sides of the condylar extremity, and makes the thickness of the shaft, where it rises at the articulation, about 3 millims. The shaft widens steadily as it extends proximally, being 1 centim. wide at 2 5 centims from the distal end The inferior lateral or anterior outline of the bone is nearly straight, becoming very slightly concave towards the proximal end, though the concavity is not more marked than that shown at the distal end. The superior lateral or posterior outline, for 2·5 centims. towards the distal end, is so gently concave as to be approximately straight; but beyond this point the radial crest widens the bone rapidly, so that at 2·9 centims. from the distal end the transverse measurement is 1·7 centim., and then the width contracts towards the articular head; but the radial crest is separated from the articular head by a concave area, which suggests a condition of connection between crest and head like that seen in the Crocodiles. The margin of the crest has two sides, which are inclined to each other at a right angle, the longer side proximal, the shorter distal and sub-parallel to the head; but the angle where the sides meet is rounded.

The head of the bone is very imperfectly preserved. It is 1 centim. wide, and gently convex from the ulnar to the radial side. The articular surface of the head is directed forward, and apparently makes an obtuse angle with the straight external inferior side of the bone. The shaft appears to have made an angle with the radial crest, but the two parts of the bone are now flattened so as to lie nearly in the same plane.

This humerus approximates in size to that of *Kistecephalus microrhinus* (OWEN) (Brit. Mus., No. 47,071), but the proximal half of that bone, which is alone preserved, shows important generic differences in a much less development of the radial crest, which is more proximal in position, and continuous with the articular head of the bone; and, judging from the position of the foramen in the shaft, the humerus of *Kistecephalus* was probably shorter than that of *Dicynodon*.

As the bone is so imperfectly exposed, it may be convenient to defer full examination of its affinities, for there can be no doubt its shape was as substantially Anomodont as the bone in other genera, though the radial crest is obviously large, and there is less indication of lateral expansion of the distal end. In these smaller and lighter bodied Anomodonts the limb bones were relatively elongated and slender; and, just as a type like *Cynodraco* has the extremities of the humerus less expanded than in *Galesaurus* and *Cynochampsa*, so it would seem that the distal expansion of the bone may be reduced in this more elongated type. There is no approximation to known Monotreme genera in the humerus. But the bone as exposed is rather suggestive of the humerus of an Ornithosaur, but apparently with the ends less twisted. The epicondylar foramen is not seen; and, on the whole, the form of the bone shows less divergence from the humerus of a Lizard than might have been expected from extreme forms which the Anomodont humerus assumes.

The Ulna and Radius.

The ulna is 3 4 centims long. It is exposed so as to show the lateral contour, which is typical of all Anomodont Reptiles, being massive at the proximal end, wide at the olecranon, with an oblique concave articulation for the humerus, limited anteriorly by a slender process, below which the shaft contracts, with slightly concave sides, before it expands slightly at the distal end to form the rounded distal extremity.

The distal condyle is nearly 6 millims wide, with a convex rounding, which is as well marked laterally as at the base. It extends proximally for 3 millims , when the shaft is narrowed to half its width. The shaft retains this width for half its length, when it begins to widen proximally, chiefly by a posterior expansion Below the articular surface for the humerus its width is 8 millims. below the proximal extremity. Then a slender process extends horizontally forward so as to widen the bone to nearly 11 millims The antero-posterior measurement of this process is hardly more than a millimetre. Its proximal aspect forms the border of the proximal articulation of the bone; its distal aspect is concave. The concave articular surface is oblique, about 7 millims. wide from below upward, so that as it ascends it somewhat reduces the width of the proximal part of the bone, which terminates in a truncated surface 6 millims. wide, somewhat obliquely inclined backward, being at right angles with the upper part of the articular surface, and rounding into the posterior surface. The proximal end of the bone appears to be but little disturbed from its natural connection with the radius, since the anterior process of the proximal articulation rests upon the radius; and this indicates that the ulna was excavated proximally to receive the radius, as in all other Anomodonts, and in a way to which some Saurischia approximate.

The radius is a shorter bone than the ulna, with the sides concave, the articular ends truncated, and the proximal end rather larger than the distal end.

The length of the bone is 3·1 centims. Its proximal end is 9 millims. wide, with the middle section of the articulation slightly convex from behind forward. The sides of the shaft approximate evenly towards each other, so that in the middle length the transverse measurement is reduced to 4 millims. The proximal half of the shaft has the external surface well rounded, but the distal end is evidently more flattened. The width of the bone at the distal end is fully 7 millims., with the anterior corner more pointed than the posterior corner, where the articular surface forms rather more than a right angle with the posterior side.

So much as is preserved of the bony tissue appears to demonstrate that these bones of the fore arm were solid, like the humerus, though in all three the external layer is thick and dense, while the middle of the shaft is more or less loose and cellular.

The humerus is flexed at rather less than a right angle to the ulna and radius, and the convexity of its distal articulation is parallel to the proximal articular concavity of the ulna, from which an interspace 3 millims. wide separates it.

It is difficult to affirm affinities from these bones. They have much resemblance to the ulna and radius among Lizards and Chelonians, but their size is too small, and exposure too imperfect, to satisfactorily demonstrate their relations to the same bones in other animals.

The Carpus

On the left side the elements of the carpus are in natural association; on the right side they are scattered, because the ulna, with one digit and part of the carpus, has been separated from the remainder of the foot by a large sub-triangular bone. It is difficult to identify the scattered bones, which appear to number about 14, while in the articulated carpus I can count but 12.

The carpus comprises three rows of bones. In the left limb there are three bones in the proximal row, such as are commonly named radiale, intermedium, and ulnare. The intermedium separates the distal ends of the ulna and radius. The radiale I regard as representing the scapho-lunar; the ulnare may be the pisiform. The second row of bones is on the radial side, and consists of three elements in linear series, which I regard as centralia; one is below the intermedium, the other two are below the impression of the radiale. In the distal row there are five or six bones. It is not possible to be sure of the exact number, for, although there are six impressions of bones, it is possible that owing to irregularity of form the appearance may be deceptive, and that two of the seemingly distinct ossifications may belong to one bone. A similar explanation would account for the apparently larger number of bones in the carpus of the right limb

Commencing with the proximal row, the radial element is represented in the left carpus by an impression, or rather a marking on the level of the surface of the slab. It is 8 millims. wide, and extends transversely beyond the radius on the inner side, and is 1 to 2 millims. deep; but in the right carpus the bone in contact with the radius is deeper, measuring about half a centimetre, by nearly a centimetre wide.

The intermedium in the left carpus is an obliquely oval sub-angular element, 6 millims wide by 4 millims. in the vertical direction. In the right carpus the same element is recognized a little to the right of the ulna. The ulnar carpal in the left carpus appears as a narrow ossification, 6 millims. in vertical measurement by 3 millims. in width at the proximal end, with the middle constricted, it is directed downward and inward as preserved. In the right carpus it is wider proximally, but its vertical extent as preserved is less. These differences in the forms of the bones are probably due to conditions of fossilization, but similar irregularities on the two sides of the body are sometimes found in the carpus and tarsus of Urodeles.

Below the intermedium, and in close contact with it is a small, nearly circular ossification, 2 millims. in diameter, which I regard as No. 1 of the central series.

No. 2, which is below the inner side of the radiale, is a polygonal and transversely oval bone, 5 millims. wide, and 4 millims. in vertical measurement. No 3 extends further on the radial side than the radiale, so that the carpus widens distally. This element is only indicated by a marking on the stone, about 6 millims long by 3 millims. vertically On the scattered right carpus there is a bone below the ulnare which may be No. 1; a larger bone below the intermedium may be No. 2; while an obviously displaced bone or two at the left upper corner of the radiale may be No. 3

The distal row of the carpus is more obscure, and may include only the normal four bones, though the number appears to be more. In the left carpus the element which corresponds in position with the trapezium appears to be ossified from more than one centre, but this appearance may be a result of fracture. It is transversely oblong, 6 millims. long, with a portion directed downward under the trapezoid. The trapezoid element is of similar form and size, though concave superiorly, and becoming narrower towards the magnum. Between these elements is a small circular ossification, 2 millims. in diameter, which is probably a portion of one or the other The magnum is a four-sided bone, nearly square, placed obliquely, 4 millims in diameter, articulating proximally with the ulnare and centrale No. 1. The unciform is a smaller bone, 3 millims. in vertical diameter by 2 millims. in width, but it is probably imperfectly preserved. In the right limb the forms of the distal carpal bones are different, and, though they appear to be more numerous, may perhaps only number four.

Owing to the condition of the bones, it is not easy to make an accurate comparison of this carpus with the same region in other animals, but on the whole it is probably best compared with that of *Hatteria* and the Tortoises The presence of centralia makes its near resemblance to the South African fossil Mammal *Theriodesmus* interesting, as a modification which is in harmony with the Mammalian character of the shoulder girdle.

The Digits.

In the left limb there is no trace of the metacarpus or digits. But on the right side, in which the ulna and radius are separated by a large bone which is possibly one of the hyoid elements, three digits lie in connection with the radius, and one with the ulna. It is possible that the first digit is imbedded in the matrix, for there appear to be indications of the first metacarpal in the slab. Nevertheless, only four digits are preserved in *Platypodosaurus*;* and the only South African fossil in which there are five digits preserved is the impression of the fore-limb figured by Sir R. OWEN† as Dicynodont, and subsequently referred with doubt to *Dicynodon*.‡

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* 'Geol Soc Quart. Journ.', vol. 36, Plate 17, "Description of Parts of the Skeleton of an Anomodont Reptile, *Platypodosaurus robustus* (Ow.), from the Trias of Graaf Reinet, S Africa," by Professor OWEN, C B, F.G S

† In his 'Catalogue of South African Reptilia' (Plate 52, figs 2, 3).

‡ 'Geol. Soc Quart. Journ', vol. 36, 1880, p 424

That specimen I regard as indicating a new genus, because the form of the humerus is distinctive, and, instead of being longer than the radius, as in other known Anomodonts, it is relatively shorter. It may be referred to as *Eurycarpus Oweni.* The number of digits is variable in other orders of Reptilia; and therefore the question must remain open whether Dicynodonts had four or five.

If the first metacarpal is present, only its proximal end is exposed in near union with the radiale a circular osseous point in advance of it might then indicate its distal end; while a somewhat larger circle prolonging the line inward would indicate the first phalange. These identifications, however, rest upon too shadowy a foundation of fact to be evidence that the digit existed.

The remaining digits are remarkable for showing a reduced number of phalanges. There are, apparently, three in the middle digit on the radial side, but only two in each of the other digits, as in terrestrial Chelonians. I number the digits 2, 3, 4, 5. The metacarpal of digit II. has a dice-box form, with large extremities. It is 8 to 9 millims. long, 5 millims wide proximally, and slightly wider distally. The third metacarpal is of similar form, about 7 millims. long; and the fourth is rather shorter, but its extremities are worn. The articular extremities appear to be more convex on the under side than on the upper side, and the proximal end is usually rather larger than the distal end.

The first phalange of digit II. is much stronger than the corresponding bones in the other digits, which decrease in size towards the ulnar side. All the bones appear to be sub-cylindrical, and contracted in the middle like the metacarpals, but are much smaller at the distal end than at the proximal end; the latter is flattened, and the former more convex. The claw phalanges are comparatively large, and as long as the phalanges which they follow; they are flattened from above downward with the superior surface convex, and apparently two grooves at the sides, such as are seen in *Iguanodon.*

If this specimen may be relied upon as a type of the Anomodontia, it makes known a very remarkable characteristic in the small number of phalangeal bones, and the small size of the foot.

The accompanying restoration of the skeleton (Plate 76) is based in its anterior part upon the bones now described, and in the vertebral column and hind limb upon fragmentary evidences from Anomodonts in the British Museum. It represents the maximum elevation of the body above the ground, such as might occur in water; but, as a rule, I regard the animal, when at rest, as lying on the ground like a Crocodile.

I would express my grateful thanks to Dr. HENRY WOODWARD, F.R.S., for the facilities afforded me in making these studies, and for permission to describe and figure the remains.

EXPLANATION OF PLATES.

PLATE 75

Slab in the British Museum (No. 49,413) showing the skull, vertebræ, ribs, scapular arch and sternal apparatus, and fore-limbs of a Dicynodont Reptile, *Keirognathus cordylus.*

Skull: *T*, temporal fossa; *O.*, orbit; *N.*, narine; *t.*, tooth; *pt*, pterygoid, *q*, quad-bone; *a.*, articular bone in the mandible.

c r., cervical ribs in contact with cervical vertebræ.

d.r., dorsal ribs.

d.v., dorsal vertebra.

Scapular arch · *s.*, scapula; *cl*, clavicle; *ic.*, inter-clavicle, *st.*, sternum, *c.*, coracoid; *pc.*, pre-coracoid, *g.*, glenoid cavity.

Fore-limb (left): *h.*, humerus; *u.*, ulna, *r.*, radius; *cs.*, carpus; the three proximal bones are regarded as ulnare, intermedium, and radiale; the three centralia are indicated as c^1, c^2, c^3; and the distal row, *Tm.*, *T.*, *m*, *u*, is interpreted as trapezium, trapezoid, magnum, and unciform.

The digits are only preserved in the right limb, where three are connected with the radius and one with the ulna, the bones of the fore-arm being separated by an undetermined bone (?) possibly the hyoid.

PLATE 76.

Restoration of *Keirognathus cordylus,* based upon the evidence of the preceding figure. The dark tint indicates the parts shown in that slab. The large size of the tooth is not quite established. The hind-limbs may have been relatively longer than is here indicated. The light parts are based upon Russian and South African evidences of Anomodont structures. When at rest the animal is regarded as having been supported upon the lower jaw, scapular arch, ribs, and pelvic bones.

XIX. *On the Skull, Brain, and Auditory Organ of a new species of Pterosaurian* (Scaphognathus Purdoni), *from the Upper Lias near Whitby, Yorkshire.*

By E. T. Newton, *F.G.S., F.Z.S., Geological Survey.*

Communicated by Archibald Geikie, *F.R.S., Director-General of the Geological Survey.*

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[Plates 77, 78.]

Introductory.

The Rev. D. W. Purdon, of Wolverhampton, obtained some years ago, from the Alum Shale[*] at Lofthouse, near Whitby, the skull of a Pterodactyl. This was brought to me last autumn, much obscured by the surrounding hard matrix. As the specimen seemed likely to repay a careful study, the owner's permission was obtained to clear away more of the matrix; and to him my best thanks are due for the very courteous manner in which he left the fossil in my hands, to be treated in whatever way was best calculated to develop its structure and add to its scientific value. By careful work with the chisel I succeeded in laying bare much more of the skull, and it has proved to be of unexpected value, and, for several reasons, of exceptional interest. In the first place, no Pterodactyl remains have previously been recorded from the Yorkshire Lias; in the second place, the form is certainly new, and seems nearly related to the Continental Oolitic species, *P. crassirostris.* Again, this skull has undergone little or no compression, and consequently the natural relations of the bones are well preserved, and the structures of the basal portions, including the palate and back of the skull, are better shown than in any Pterosaurian from this side of the Atlantic hitherto described.[†] And still further, the form of the brain and parts of the auditory organ being preserved, their structure and relation to the entire skull can now be studied in a manner not previously possible.

Description of Skull.

This Pterodactyl skull, in its present condition, measures five-and-a-half inches in length (140 mm.); but, as the snout, from just in front of the nasal apertures, is

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[*] My colleague, Mr. Barrow, tells me this must be the Alum Shale of the Upper Lias

[†] The skull of *Pteranodon longiceps*, as given by Professor Marsh, seems to be in a very perfect condition; but it has not yet been fully described. See 'Amer. Journ. Sci.,' vol 27, 1884, p. 423.

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wanting, its proper length is uncertain—probably, when perfect, it was about two inches longer. The extremely thin outer plates of the bones are almost all broken away; this, however, is not altogether a disadvantage, for not only has it exposed several casts of the air cavities, that seem to have occupied the interior of every bone, but the margins of many of the bones are now shown, which, if the external layer had been intact, would probably have been obscured. Both sides of the skull are somewhat broken, but what is wanting on one side is preserved on the other. The supra-occipital region was also broken away when the specimen came into my hands. In a lateral view (Plate 78, figs. 2, 3) there are five distinct apertures. The anterior one is the elongated nasal aperture (*e.n*), behind this is the somewhat larger ant-orbital fossa (*ant. orb.*) or median aperture; and then comes the orbit (*orb.*), the last named being the largest of the five. Behind the orbit are the infra-temporal fossa (*inf. tem.*) and the supra-temporal fossa (best seen in Plate 77, fig. 1, *sup. tem.*), and these are smaller than any of the other three.

The whole of the snout in front of the nasal apertures seems to be formed by the premaxillæ (*pm.*), which bound these openings anteriorly and above; on the palate (fig. 4) they are firmly united, and form a plate of bone extending from one alveolar margin to the other, these margins standing as a ridge on each side, with a shallow depression running along just within them. Another groove runs along the middle, deepening as it approaches the internal nasal apertures A slight ridge is seen in the middle of the groove, which passing back, joins what is evidently the vomer (*vo.*). The bony palate extends backwards for some distance on the outer side of the internal nares; but it seems probable that the portion behind the line seen passing obliquely forwards and outwards from each of these apertures may be a palatal portion of the maxilla. If this be so, then some of the teeth probably belonged to the maxilla.

On the middle of the upper surface of the skull (fig. 1) a long tract of bone, which I believe to be an extension of the premaxillæ, runs backwards, and, separating the nasals and pre-frontals, reaches the frontals at about the anterior third of the orbit. On the outer side (fig. 3) the premaxilla, after forming the lower boundary of the external nares for about three-fourths of an inch, seems to overlap and lie external to the maxilla, but how far it extended backwards is uncertain, possibly it may have run some distance below the ant-orbital fossa. On the right side, the alveoli for four flattened teeth may be seen. The first, at the extreme end of the specimen, is small, having a long diameter of 2·5 mm.; after an interval of 5·0 mm., there is a second alveolus, with a long diameter of 5·0 mm. and a short diameter of 3·5 mm. Another interval of 6·0 mm., and a third alveolus of 4·0 mm.; again, a space of 6·5 mm., and then the fourth alveolus, 4·2 mm. in diameter. On the left side traces of similar alveoli are seen, but they are less perfect.

The right maxilla (fig. 3, *mx.*) is better preserved than the left, and its front part appears to be on the inner side of the premaxilla, but the junction of the two bones is very obscure, as it is in Birds. Posteriorly the maxilla has two processes; one extending upwards and backwards forms the hinder two-thirds of the lower boundary of the nasal aperture, and then joins the bone which is believed to be the lachrymal, above the ant-orbital fossa. The second or lower process is narrow and extends backwards to the jugal region. At this point, on the right side, the maxilla is broken away; but the portion here wanting is present on the left side (fig 2), where it comes below the lower angle of the jugal (*ju.*), and seems to meet the quadrato-jugal (*qu ju.*). The jugal is a V-shaped bone (fig. 2, *ju*), forming the lower boundary of the orbit; one limb, passing upwards in front of the orbit, meets the lachrymal; the other limb rises behind the orbit, and has its posterior edge occupied by the quadrato-jugal On the right side (fig 4) the lower part of the jugal is seen to be inclined forwards and to lie on the inner side of the maxilla. This V-shaped jugal is quite unlike any of the bones in a Bird's jugal arch, but in *Chamæleo, Lacerta agilis,* and other Lizards* the jugal bone has a somewhat similar form, extending backwards from the lachrymal below and then upwards behind the orbit, where it meets the post-orbital. The quadrato-jugal (fig. 2, *qu. ju*) forms a vertical triangular plate behind the jugal, the base of the triangle being below and the apex extending upwards to meet the post-orbital (*pt o.*). From the lower and hinder part of the quadrato-jugal a splint of bone runs up the front and outer margin of the quadrate (*qu.*). On the right side (fig. 3) the jugal, quadrato-jugal, and quadrate are much broken. In all Birds the quadrato-jugal is a slender bone and quite unlike this bone in the Pterodactyl, while it is wanting in all Lizards except *Sphenodon,* and in this the lower temporal bar is formed by the jugal bone, while the quadrato-jugal is fixed to the outer side of the quadrate.† The Yorkshire Pterodactyl has the lower temporal bar much reduced in antero-posterior extent, while its distance from the supra-temporal bar is proportionately greater, it is not surprising, therefore, to find the quadrato-jugal, as well as the jugal, with a greater vertical than horizontal extent.

At the hinder end of the external nostril on the left side (fig. 2, *en.*) there is a portion of a bone (*na.*) which, when perfect, probably extended from the premaxillary process above to that of the maxilla below, thus forming the hinder boundary of the nasal aperture, and sending backwards a narrow slip between the lachrymal (*la.*) and pre-frontal (*p.fr.*), terminated just in front of the anterior corner of the orbit. This bone occupies the position of the nasal.

Two elongated convex tracts seen on the upper surface of the skull are thought to indicate the positions of two large pre-frontals‡ (figs. 1, 2, and 3, *p.fr*), which would thus be separated from each other by the long premaxillary processes; anteriorly and externally they are bounded by the nasals, and posteriorly by the frontals (*fr.*), each of which sends forward a slender process separating the pre-frontal from the orbit

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* PARKER, 'Phil. Trans,' 1879, Plate 42, fig 3, and 'Zool Soc. Trans.,' vol 11, 1881, Plate 16, fig 1.

† BAUR, 'Zoologischer Anzeiger,' No 238, 1886.

‡ Since the above was written I have had the opportunity of showing the specimen to Dr. G BAUR, of Yale College, who has so carefully studied the skull of *Sphenodon;* and he suggests the possibility of the area, which I have, with some doubt, called pre-frontal, being only part of the bone marked as nasal. It is by no means clear that these two areas can represent a single bone, but, if they do, then there will be no distinct pre-frontal bone —E. T. NEWTON, *Sept* 25, 1888.

The frontal bones themselves occupy the upper part of the skull between the orbits, of which they form the upper boundary, how far they extended backwards is uncertain, as the parietal and supra-occipital regions have been broken away, but probably they covered the whole of the cerebrum (*cb.*). In the front region of each cerebral lobe the inner and outer tabulæ of the frontal bone, when perfect, evidently met, and, shutting out the air cavity at this point, apparently formed one thin bony plate.

Within the anterior angle of the orbit (figs. 1, 2, and 3) lies the excavated hinder end of a bone (*la.*) which extends forwards, below the nasal bone, to meet the superior process of the maxilla (*mx.*), and downwards along the front border of the jugal, thus forming the upper and hinder boundary of the ant-orbital fossa. This bone has the characters and relations of the lachrymal.

The upper and hinder margin of the orbit is separated from the supra-temporal fossa by a buttress of bone, springing from the hinder frontal region, which occupies the position of post-frontal and post-orbital bones, and may include both these elements, as in *Sphenodon* * Externally this buttress arches downwards, and meets the ascending process of the quadrato-jugal, and possibly that of the jugal also. To what extent the post-orbital enters into the formation of the supra-temporal bar is uncertain, no sutures being seen; but probably the post-orbital and squamosal form about equal parts. In *Sphenodon* the triradiate post-orbital (marked *m.* by Dr GUNTHER) meets the squamosal to form this bar; and Professor W. K. PARKER† has shown that the same arrangement occurs in the Chameleon. Moreover, the skulls of *Pterodactylus crassirostris*‡ and *Dimorphodon macronyx*§ both appear to have the supra-temporal bar formed in this same manner.

The supra-temporal fossa is bounded behind by another buttress of bone, the upper part of which arises from the parietal region of the skull (figs. 1 and 5), and the lower part is in close relation with the auditory capsule. Judging from the intimate structure of the skull in *Chamæleo*, *Lacerta*, and other forms of Lacertilia, with which Professor PARKER has made us so fully acquainted,‖ the upper proximal part of the bar will be formed by the parietal, and this, resting upon the auditory capsule, will probably include parts of the otic bones. The external part of the bar is no doubt formed by the squamosal, which gives a point of attachment for the quadrate, and doubtless forms, with the post-orbital, the supra-temporal bar. The squamosal, as we shall presently see, is supported behind by the parotic process, which wraps round the upper part of the quadrate. The post-temporal fossa (fig. 5, *pt.fos.*), which is so well seen in *Sphenodon* and is extremely large in the common Chameleon, is here very small, being reduced to an oval slit.

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* See GÜNTHER on *Hatteria*. 'Phil. Trans.,' 1867, pt. 2, Plate 1, fig 4, bones marked *l.* and *m.* Also, BAUR, 'Zoologischer Anzeiger,' No. 240, 1886.

† 'Zool. Soc. Trans.,' vol. 11, 1881, Plate 16.

‡ GOLDFUSS, 'Nova Acta Leopold.,' vol. 15, 1831, Plates viii. and ix.

§ OWEN, 'Palæontogr. Soc.: Reptiles of the Lias,' Plate 20, 1869.

‖ 'Phil. Trans.,' 1879, p. 595; and 'Zool. Soc. Trans.,' vol. 11, 1881, p. 77.

The base of the cranium (figs. 4 and 5) is remarkable in that its height is greater than its antero-posterior extent. At the back there is a broad plate of bone, about 13 mm. wide, which extends from the foramen magnum downwards and forwards for about 15 mm The occipital condyle is wanting; but on each side, and a little below the level of the foramen magnum, there is a large and deep depression; doubtless it is the foramen for the exit of nerves (probably ninth, tenth, and twelfth). Near the middle of each side of the flattened base there is a prominent rounded process. Below this the base narrows somewhat, and from its lower and anterior edge two long rod-like bones or processes (*bp p.*) pass down to the inner angle of the quadrate. This is very like the base of the Chameleon's skull, except that it is more nearly vertical, and doubtless, like it, includes the basi-occipital and basi-sphenoid, as well as parts of the exoccipitals; but no sutures remain to show the extent of each. The long rods are probably the homologues of the basi-pterygoid processes of the sphenoid, but their great length suggests the possibility of their being separate bones. The front of the basi-sphenoid descends almost vertically, and then curves forwards as it divides into the two basi-pterygoids.

On each side of the foramen magnum there is a large paroccipital process (fig. 5, *op.ot.*), which extends outwards, leaving an oval space between itself and the post-temporal buttress, but towards its distal extremity it expands into a broad fan-like plate, which is applied against the hinder and outer part of this buttress and wraps round the head of the quadrate, holding the latter bone, immovably as it seems, against the squamosal. Precisely similar paroccipital processes are developed in Lizards, and Professor PARKER[*] has shown that they are mainly formed by the opisthotic bones, the basal portion of each containing the lower and hinder parts of the posterior and horizontal semicircular canals The exoccipitals only form a small part of the base of these processes. In the fossil the auditory semicircular canals have been traced (see p. 511), and are found to have this same relation to the base of the paroccipital process. At the outer end of each paroccipital process, and forming the hindermost angles of the skull, there seems to have been a small separate bone, which occupies the position of and probably is the supra-temporal, a bone said to be constantly present in Lizards.

The front and side of the brain case have been exposed by clearing away the matrix from the orbit and temporal fossa on the right side, and its relatively small size is shown in fig. 3*a*, where it is represented without the supra-temporal bar, so as to show the parts more clearly.

The sides of the cranium are completely ossified, but in front there is a large rounded aperture. Through the lower part of this opening, no doubt, the optic nerves passed; and it is tolerably certain, therefore, that the pre-sphenoids and orbitosphenoids were not ossified. A little below the large front opening, and towards the side, is an aperture completely surrounded by bone, through which in all probability the fifth nerve passed out of the cranium (Plate 78, fig. 3*a*, *v*)

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[*] *Loc cit*

The quadrate forms a broad extent of bone, seen chiefly at the back of the skull (figs. 2, 4, and 5, *qu*) Its hinder part is convex from side to side, the inner and outer margins being directed forwards; but, although wide, it seems to have been extremely thin, appearing upon the side of the head merely as a slender rod (fig. 2). Its upper part is narrow, and wedged in between the squamosal and the broad end of the opisthotic or paroccipital process. Passing downwards, it rapidly widens, leaving a comparatively small space between its upper part and the base of the skull (fig. 5). The articulation for the lower jaw is wanting, but, judging from other specimens, little more than the rounded surface has been lost. The inner and lower extremity of the quadrate is continued directly into the pterygo-palatine bar (fig. 4), the impressions of the bones at this point showing no indication of a division, the quadrate and pterygoid apparently being firmly attached, if not ankylosed. The basi-pterygoid process meets the quadrate and pterygoid at their point of union, but, being broken at this part, one cannot say whether they were fixed to each other, although the manner in which the basi-pterygoid lies close along the inner edge of the distal part of the quadrate makes it probable that they were immovably attached.

Directly in front of the quadrate the pterygo-palatine bar widens, but the form of the bone at this point is uncertain, as it is somewhat broken; however, it is clear that it formed a thin plate extending forwards to the point marked *pl.* (fig. 4). The inner edge of this plate is thickened, and extends forwards continuously until it meets the triangular plate in the middle line (*vo.*), which there can be little doubt is the vomer. The outer margin of the pterygoid portion of the bar is also thickened, and at a distance of about 15 mm. from the quadrate comes very near to the slender extremity of the maxilla. Some markings on the matrix at this part seem to indicate the former existence of bone, which may have been a transpalatine. GOLDFUSS has described in *P. crassirostris* a portion of bone in this position, which he calls a transverse bone.* The thin plate of the pterygo-palatine bar is nearly horizontal just in front of the quadrate, but, as it passes forwards, the outer edge descends and the inner rises a little towards the roof of the skull, thus tilting the plate, and at a distance of about 25 or 30 mm. from the quadrate it divides into an inner and an outer portion, the slender inner rod extending to the vomer, as already noticed, while the outer portion, becoming more inclined, rapidly assumes a vertical position, and passing forward, evidently joins a palatine plate of the maxilla. The actual junction of these two bones is not seen, but they can be traced to within 6 or 7 mm. of each other, and then a small piece has been broken away. The long aperture (about 35 mm.) enclosed by the palatine behind and the maxilla with the vomer in front is, without doubt, the internal nares (fig 4, *in*), and anteriorly it is only separated by the vomer from the corresponding aperture of the opposite side. The front of the internal nares is about 32 mm further back than the front of the external nares

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* 'Nova Acta Leopold.,' vol. 15, 1831, p. 76.

The absence of any traceable division in what has been called above the pterygo-palatine bar, and the large size of the basi-pterygoid process (*bp p*), leads one to question whether the last-named bone may not be the pterygoid, and the bar in front of the quadrate the palatine only. In the first place, it must be remembered that the fixity of all the bones of the Pterodactyl skull, and as a consequence the ankylosis of many of them, makes it probable that the bones of the palate would become soldered together, and this certainly seems to have taken place at the junction of the quadrate with the bones of the palate The manner in which the front part of the bar bounds the hinder end of the internal nares leaves no doubt as to this portion being the palatine, and as the normal position of the pterygoid is between the palatine and quadrate, the hinder part of the bar is believed to be the pterygoid. It is true the pterygoid bone sometimes extends from the quadrate to the base of the skull, as in many Birds, but even when this is the case it still separates the palatine from the quadrate I am not aware of any case among Reptiles or Birds where the palatine comes into relation with the quadrate to the exclusion of the pterygoid. That the basi-pterygoid process may be much elongated is seen among Birds in the Emu* and among Lizards in the Chameleon† In the Emu the relations of the bones are strikingly similar to what is seen in this Pterodactyl, for the long basi-pterygoid abuts upon the hinder end of the pterygoid close to the quadrate, just as in the fossil. The basi-pterygoid of the Chameleon is similarly long, and directed forwards to support the pterygoid, while a backward process of the latter extends to the quadrate. Taking into consideration the arrangement of the bones which we know occurs in Birds and Lizards, it seems much more in accordance with them to regard the bone which, in this Pterodactyl, extends from the base of the skull to the quadrate as an elongated basi-temporal process of the basi-sphenoid, and the bar in front of the quadrate as the combined pterygoid and palatine bones.

DESCRIPTION OF THE BRAIN.

When this Pterodactyl skull was first brought to me, the fracture of the parietal and frontal bones had exposed a part of the cast of the cranial cavity in the cerebral region, and it seemed likely that a cast of the whole interior of the skull had been preserved. The small relative size of the cranium made it highly probable that the brain had originally filled the cavity, and, if so, the cast would give the form of the brain. To expose this cast on one side, I obtained Mr PURDON's permission to remove a portion of the bone, and having raised the greater part of the left frontal in one piece, little by little other parts were cleared away, until I had succeeded in exposing not only the cast of the left half of the brain, but also a large part of the auditory organ. The form of the cast exposed leaves no doubt but that it represents the form of the Pterodactyl's brain, just as much as would a cast taken from the skull of a Bird or Mammal; and such casts show the natural external form of the brain even better than a brain itself, which, being very soft, is apt to be distorted and shrunken by the means adopted for its preservation. Taking the cast, therefore, as representing the brain (figs. 1, 6, and 7), it will be seen to be relatively small, its greatest length, from the edge of the occipital foramen to the front of the cerebral lobes, being 25 mm., and its greatest width—that is, across the optic lobes—17 mm.; it is therefore about one-sixth or one-seventh the length of the entire skull. Each cerebral lobe is a somewhat depressed egg-shaped mass, wide behind, narrow in front, and separated from its fellow by a deep groove, which is naturally occupied by the inner edges of the frontals, anteriorly, it is continued into a small triangular olfactory lobe, which can be traced for about 5 mm. in front of the cerebrum. The thickness of each cerebral lobe is not quite as great as its width (fig. 6), and below, at about its hinder third, there is a depression or fissure. A large optic lobe is placed directly behind the cerebral hemisphere, and is separated from it by a well-marked groove, which is seen on the side of the brain running upwards and backwards, and then over the upper surface to within 5 mm. of the middle line (fig. 7); the optic lobe itself extends a little further inwards, and is then broken away, its height being a little greater than that of the cerebrum. A second and shallower depression, seen on the upper surface of the brain, running round the back of the cerebral lobe, marks off a triangular space

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* HUXLEY, 'Zool Soc Proc,' 1867, p. 422.

† PARKER, 'Zool. Soc Trans,' vol 11, 1881, Plate 19, fig 2.

Unfortunately, the cerebellum is almost wholly wanting, and this is much to be regretted, as it is the relation of this to the optic lobes which is of so much interest when the possible relations between Birds and Pterodactyls are discussed. However, we are not without some indications of its position, for on the right side, at the point marked *cbl* (figs. 1, 6, and 7), a fragment of the cerebellum marks its hinder boundary to very nearly the middle line; on the left side, the optic lobe is preserved to within 4 mm. of the middle line; and between the hinder part of the cerebral lobes there is a small triangular rising, occupying the position of a pineal lobe. The hinder boundary of the cerebellum is fixed, and it is also certain that it cannot have extended beyond the other points just noticed, and may not have extended quite so far. The greatest length of the cerebellum could not have been more than 10 mm. or its width more than 7 mm. It is tolerably clear, however, that the cerebellum extended between the optic lobes, somewhat as in Birds, and that the optic lobes did not separate the cerebrum from the cerebellum, as they do in all Reptiles.

Being anxious to corroborate this extension of the cerebellum between the optic lobes, I examined the Pterodactyl skulls in the British Museum, but without success. Mr. R. Lydekker, however, showed me a specimen in the Fox collection which included a cranium; and Dr. H WOODWARD, with his usual courtesy, had the specimen cut through longitudinally in the middle line This section exhibits the brain cavity under a considerable thickness of open cancellous bone. The upper part of the cavity forms a double arch, one curve extending from the foramen magnum upwards and forwards for nearly half the length of the cavity, while the second and rather longer curve continues from this to the front The section being in the middle line, the anterior of these curves will be between the cerebral lobes, and consequently does not give their proper convexity, although showing their antero-posterior extent. The hinder curve, as I understand it, is that of the cerebellum; for if the optic lobes in any part came between the cerebrum and the cerebellum, some slight indication of them ought to be seen by a break in the curve where the cerebellum ended No such mark is seen, and I conclude, therefore, that the cerebellum reached to the cerebrum in this Wealden specimen, and probably also in that from the Yorkshire Lias.

A little behind the optic lobe, and separated from it by a definite space, there is a large pyriform flocculus (figs. 1, 6, and 7, *fl.*). This body, which is somewhat flattened from above downwards, is attached by its broad end to the side of the hind brain just below the cerebellum, and is directed outwards and backwards. Until exposed by the chisel the flocculus was contained in a cavity of the bone situated in the base of the hinder supra-temporal buttress at its junction with the opisthotic, and, consequently, immediately on the inner side of the post-temporal fossa (fig. 5), from which it was separated only by a thin plate of bone. The lower and outer edge of the flocculus is marked by a depression or groove, which divides it into a larger proximal and a smaller distal portion. The finding of this flocculus was as advantageous as it was unexpected, for although not seen in Lizards, it is present in Birds, and has served as a landmark in exploring the auditory region.

SENSORY ORGANS.

If the interior of a Bird's skull be examined, such as that of a Goose, there will be found on each side, in the region of the auditory organs, a large recess hollowed out of the bony periotic capsule. (A similar cavity is found in some Mammals, such as the Rabbit.) This recess, as is well-known, is occupied by a lobule given off from the side of the hind brain, called the flocculus; and around it the various parts of the internal ear are arranged. Just below the entrance to this cavity are the foramina for the auditory nerves passing to the vestibule, which lies just below the inner part of the flocculus. The anterior vertical semicircular canal arches over the entrance to the recess, close to the inner side of the skull, and the posterior vertical canal forms an arch just behind it; while in a plane a little below and underneath it, the horizontal canal forms a segment of a circle, with the convexity turned outwards.

In clearing away the bone of the fossil surrounding the flocculus of the left side, a small tube filled with black matrix was found, arching over the pedicle of the flocculus and dipping down between it and the optic lobe. This canal was removed from the left side, but its fellow is still seen in place on the right (figs 1 and 7), and its position is precisely that of the anterior vertical semicircular canal of a Bird. By carefully tracing this tube backwards and downwards another was uncovered, joining it and forming an arch behind the flocculus corresponding in position with the posterior semicircular canal of a Bird. Having thus uncovered two of the canals, it seemed very probable that the third would be found under the flocculus. The exploration here was more troublesome, as it was necessary to dig somewhat under the flocculus; but a portion of a horizontal tube was at length discovered, which, although seemingly larger than the two placed vertically, is believed to be part of the horizontal semicircular canal. The front limb of the anterior canal seems to be enlarged at its lower part, but of this one cannot speak with certainty; and a similar enlargement is seen at the lower end of the hinder limb of the posterior canal. These enlargements, it will be noticed, are in the same positions as the ampullæ in Birds; and indeed the close resemblance, in all essential particulars, which these canals in the fossil bear to those of the auditory apparatus of Birds, leaves no room for doubting that they had a similar function.

With regard to the fenestra ovalis we can now speak with confidence. The quadrate and base of the skull being so similar in the Pterodactyl and in the Chameleon led one to expect that the fenestra ovalis would have a similar position in both; and when the matrix was cleared away from the right side of the base of the fossil skull, within the temporal fossa, this aperture was found in a deep hollow just in front of the lower part of the paroccipital process (fig. 3*a*, *fo.*). GOLDFUSS in his description of *Pterodactylus crassirostris** noticed an aperture in this position which he thought might be the opening of the ear.

In Lizards which have an ear-drum the quadrate is curved over and forms an attachment for it; but in the Chameleon, which has no external drum, the quadrate is straight and the outer end of the stapes abuts upon its inner side. In the Pterodactyl the quadrate is similarly straight, and the fenestra ovalis is, in like manner, partly hidden behind it, and, from this resemblance in structure, it seems fair to infer that this Pterodactyl, like the Chameleon, had no ear-drum.

The sense of vision seems to have been keen in the Pterodactyl, for the orbits are wide, and the large size of the optic lobes may probably be taken as an indication that the eyes were well-supplied with nerves. No sclerotic plates were found in this specimen, although careful watch was kept for them when clearing the matrix from the orbit.

The large size of the external nares might be thought to indicate a corresponding development of the sense of smell; but the olfactory lobes are too small to justify such a conclusion.

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* 'Nova Acta Leopold.,' vol. 15, p 72, Plate viii.

SYSTEMATIC POSITION OF THE YORKSHIRE PTERODACTYL.

In considering the relation which this Pterodactyl bears to other Pterosauria, we may at once dismiss all the Cretaceous species, for the American forms are characterised by the absence of teeth, as well as by other peculiarities of the skull, while the British species which are represented by portions of the skull, so far as they are known, have a ridge along the palate, and the anterior premaxillary teeth directed forwards. The anterior part of the snout being lost in the Yorkshire specimen, we do not know whether there were teeth in front or whether it terminated in an edentulous beak, as in *Rhamphorhynchus*, but the large size of the external nares and ant-orbital fossæ prevents a reference to that genus. Nearly all the forms which are generally placed in the genus *Pterodactylus* have the nasal aperture larger than the ant-orbital fossa, the latter being very small, and in most cases the two spaces are not separated by bone. Our fossil, therefore, will not agree with any of these.

There are two forms to which the Yorkshire fossil bears a closer resemblance, and these are *Dimorphodon macronyx* and *Pterodactylus crassirostris.* The former, being from the Lias, may be first considered. *Dimorphodon* * is characterised by the presence of two forms of teeth in the lower jaw, a few larger ones in front, and numerous small ones just within the edge of the hinder part of the jaw. Whether the Yorkshire specimen had these two kinds of teeth or not we do not know, and in the absence of this character, on which the generic distinction of *Dimorphodon* largely rests, one could hardly refer it to that genus, even if their resemblances were greater than they are; but it will be seen that the proportions of the skulls are quite different, as well as the relative sizes of the lateral apertures. In *Dimorphodon* the nasal aperture is larger than the ant-orbital fossa, while the orbit is smaller than either of them. In the Yorkshire skull the proportions are reversed, the nasal aperture being the smallest and the orbit the largest of the three. The great height of the skull of *Dimorphodon,* in proportion to its length, and the slenderness of all the bones are quite unlike the Yorkshire fossil. Although these characters by themselves might not be deemed sufficient for generic distinction, yet, seeing that the form next to be noticed makes a still nearer approach in the structure of its skull, one cannot but give the preference to that genus.

Pterodactylus crassirostris from the Lithographic Slates, as figured by GOLDFUSS,† VON MEYER,‡ and OWEN,§ certainly makes a nearer approach to our fossil than does any other form yet described, and a comparison of the figures just referred to with those here given (figs. 1–5) will show the close resemblance between them. The general form is very similar, and the relative proportions of the lateral apertures are the same in both, indeed, so close is the agreement that the two cannot be generically separated, although there are points of difference which militate against their belonging to the same species

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* OWEN, 'Palæontogr Soc · Reptiles of the Lias,' 1869 and 1874.

† 'Nova Acta Leopold,' vol. 15, part 1, p. 63, Plate 7.

‡ 'Fauna d. Vorwelt,' p. 40, Plate 5.

§ 'Palæontogr Soc.: Cret Rept,' 1851, Plate 27, figs. 2, 3, 4.

The somewhat crushed condition of the skull of *P crassirostris* makes its true form a little uncertain, yet it seems tolerably evident that it was originally more depressed than in our fossil; it has a median ridge extending, apparently, from the snout to the parietal region; and the ant-orbital fossa is somewhat triangular. The Yorkshire specimen, on the other hand, has the ant-orbital fossa more oval, and there is a definite channel along the middle of the upper surface of the skull, between the large pre-frontals and continued over the frontals as far as they are preserved, the teeth also seem to have been more numerous than in *P. crassirostris.*

These differences prevent the two specimens being placed in the same species, and their wide separation in time makes it still more certain that they are distinct forms.

Pterodactylus crassirostris, GOLDFUSS, has been thought by several writers on the Pterosauria to exhibit characters of the skull and other parts of the skeleton justifying its generic separation; and in the year 1843 Professor FITZINGER* proposed for it the name of *Pachyrhamphus,* while in 1861 Professor WAGNER† suggested that of *Scaphognathus.* Mr. R. LYDEKKER has pointed out to me that Professor FITZINGER's name, having already been used for a genus of Birds, is preoccupied and cannot be adopted, although it has the priority, and Professor WAGNER's name, *Scaphognathus,* must therefore be used.

I purpose naming the Yorkshire Pterodactyl after the gentleman to whom it belongs, as an acknowledgment of his patient kindness, which has permitted me to keep it sufficiently long to work out its points of interest, and to lay the results before the Royal Society; its name, therefore, will be *Scaphognathus Purdoni.*

COMPARISON OF SCAPHOGNATHUS PURDONI WITH OTHER PTEROSAURIANS.

The skulls of Pterosauria, hitherto described, are for the most part in a condition which renders a close comparison with *S. Purdoni* of little value; but still there are two or three forms which may with advantage be so compared. Taking, in the first place, *Dimorphodon macronyx,* one can fully appreciate Sir R. OWEN's difficulty as to the extent of the maxilla, the terminations of which are so much obscured by the overlapping of the neighbouring bones. If my interpretation of the bones of *S. Purdoni* be correct, then the bone marked by Sir R. OWEN, No. 15 (nasal)‡ may possibly include also the pre-frontal, and the element marked No 14 (pre-frontal) may be the lachrymal. The region in *D. macronyx* between the numbers 21 and 26 is so like the corresponding part of *S. Purdoni* that it will probably be found to include parts of both jugal and quadrato-jugal. The supra-temporal bar of *D. macronyx* was probably formed of two parts, as restored by Sir R. OWEN (*loc cit.*), but it is not easy to distinguish these elements in the specimens themselves, and it seems most probable, as already stated (p 506), that the hinder of these two bones is the squamosal. The rod marked No. 27 (squamosal) in Sir R. OWEN's restoration occupies the position of the bone which in *S. Purdoni* I have called the basi-pterygoid, and that numbered 28 (tympanic) is what we now commonly call the quadrate.

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* 'Systema Reptilium,' p 35.

† 'München, Bayer. Akad. Sitzber,' Jahrg. 1861, vol 1, p. 518.

‡ 'Palæont. Soc., Lias Rept.,' 1874, Plate 20.

Not having seen the original specimen of *S. crassirostris*, I am only able to make comparison with the figures and restorations published by GOLDFUSS.* There is in this specimen the same uncertainty as in *D. macronyx* as to the extent of the nasal and pre-frontal bones, and also of the premaxilla and maxilla. There can be no doubt that the bar of bone separating the nasal aperture from the ant-orbital fossa is formed by the maxilla and not by the premaxilla, and it seems probable that the hinder bar of bone† is also a part of the maxilla; but, as we have seen in *S Purdoni*, it is quite possible that the premaxilla may extend backwards for some distance on the outside of the maxilla The oblique line seen below the ant-orbital fossa is, I think, correctly interpreted by GOLDFUSS as the junction of the maxilla and jugal bones, the last-named bone being marked *m* by GOLDFUSS and 21 by OWEN. If this region of the skull is formed as in *S. Purdoni*, and the general resemblance makes this almost certain, then the bone marked *g* by GOLDFUSS and 27 by OWEN in his figure 3 will be a portion of the quadrato-jugal. GOLDFUSS described the jugal arch as consisting of two parts. The inner angle of the quadrate is seen to meet the long process from the basi-sphenoid, as described by GOLDFUSS,‡ which process I should interpret as the basi-pterygoid process, at this point also it meets the hinder part of the bar of bone seen in the orbit and crossing the ant-orbital fossa. GOLDFUSS fully described this bar as including pterygoid, palatine, and transverse bones, an interpretation fully borne out by the study of *S. Purdoni*. The slender rods of bone, one of which projects below the angle of the jaw, are no doubt correctly described as parts of the hyoid.

In Professor QUENSTEDT's account of *Pterodactylus Suevicus*,§ the skull was fully described, and in 1871 Professor H. G. SEELEY|| gave a translation of this description and suggested some modification in the interpretation of the bones. It is acknowledged that the skull of this specimen is much pressed and twisted, and consequently the parts are somewhat out of place. *P. Suevicus* evidently had a long skull, the snout being proportionately more slender than in *S. Purdoni*, and more resembling that of

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* 'Nova Acta Leopold.,' vol. 15, Part I., Plates 7, 8, 9, 1831 Reproduced by OWEN, 'Palæont. Soc.,' 1851, Plate 27, figs 2, 3, 4.

OWEN, *loc cit.*, fig. 3, No 22

‡ *Loc. cit*, Plate 7, *i*.

§ 'Ueber *Pterodactylus Suevicus*,' 4to, 1855.

|| 'Ann Mag. Nat Hist,' ser. 4, vol. 7, p. 20

*P. longirostris.** Not having the original specimen for comparison, I may, perhaps, be mistaken, but I cannot understand why the lateral apertures of the skull should be differently interpreted from what they are in *P longirostris.* There is the same large anterior, or nasal, aperture (through which the bones numbered 16 are seen), and the hinder rounded aperture or orbit; between these are two processes projecting from the upper margin, which it is difficult to understand, if they are not the same as those which in other Pterodactyls mark the front and back of the ant-orbital fossa, or "middle hole" of the skull. The so-called nasal slits on the upper surface of the premaxillary region may be due to crushing, they are certainly very small for the anterior nares and are not seen in another specimen of the species noticed below. The bone numbered 3 by Professor QUENSTEDT is surely the premaxillary process, and not the nasal bone, the latter being in all probability the bone marked 2. According to this interpretation, number 19 will mark the process of the maxilla which separates the nasal aperture from the ant-orbital fossa. Number 26 is no doubt correctly named the quadrate, and the bone extending forward from this, and numbered 16, is the pterygo-palatine bar. I cannot think that either of the bones marked 25 can be a pterygoid, for it would then be more out of place than the palatine and quadrate, between which the pterygoid properly lies; and, moreover, the hinder end of the bone, number 16, is already in the place of a pterygoid. The hinder part of the head is much broken, and the bones numbered 25 may, perhaps, be parts of the jugal or supra-temporal bars.

Another specimen, referred to *P. Suevicus*, has been described by Dr. OSCAR FRAAS,† and this shows nothing of the slits which, in Professor QUENSTEDT'S specimen, were thought to be the nasal apertures. The brain case seems to be entire, and shows the supraoccipital region extending backwards, but not so much as it seems to do in the type specimen The bones in the middle region are distinct, but so much out of place as to make their interpretation very uncertain. The lower of the two bones marked *fr.* is, I believe, the lower temporal bar, and apparently indicates also the presence of a supra-temporal bar in this species, as in *P. crassirostris.*

The remarkable toothless Ornithosaurians, described by Professor MARSH, from American Cretaceous beds, may be noticed here, although very unlike *S. Purdoni* in the details of their structure. The most striking peculiarity of these skulls, besides the absence of teeth, is their enormous crest-like extension backwards from the occipital region; a structure reminding one forcibly of the skull of the Chameleon,‡ where the supra-temporal fossæ are greatly enlarged by the extension backwards of the supra-temporal bar and the middle region of the skull; but in *Chamæleo pumilus*, while there is a similar development of occipital crest, the supra-temporal fossæ are covered over above by bone, and this is the condition which is found in *Pteranodon*;

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* See GOLDFUSS, 'Nova Acta Leopold,' vol. 15, Plate 10; and OWEN, 'Palæont Soc.,' 1851, Plate 27.

† 'Palæontographica,' vol. 25, 1878, p. 163.

‡ Professor W. K. PARKER, 'Zool. Soc. Trans.,' vol. 11, 1881, p 77.

but in the latter the crest is much larger, and the supra-temporal fossæ are so completely covered in by bone that only a small post-temporal fossa can be seen in the published figures *

Professor SEELEY, in his work on Ornithosauria,† described two portions of skulls and the cast of a portion of a brain cavity, from the Cambridge Greensand, as remains of Pterodactyl, giving evidence of the form of the brain. These specimens, with the addition of a frontal bone, were further described in 1871, and from this evidence, restored figures of the brain were given ‡ In another communication on the same subject§ one of these specimens was omitted, as it was thought to be part of a Bird; and as such was described with other Avian remains.|| The second portion of skull¶ still referred to Pterodactyl, I have carefully compared with the Yorkshire specimen, and am inclined to agree with Professor SEELEY'S identification, but its fragmentary condition prevents, as it seems to me, a definite determination, and possibly it may be Avian. The cast figured on the same plate (figs 10, 11, and 12) represents a pair of cerebral lobes, and perhaps a part of the cerebellum behind and between them, and in form agrees fairly well with the form of the cerebral lobes in *S. Purdoni.*

The indications of the form of the brain, shown by the portion of skull,** are not sufficient to allow of comparison with *S. Purdoni*; the rounded bodies seen at the sides are doubtless a pair of optic lobes, but unfortunately we cannot see how far they extended up the sides of the brain; they seem, however, to be more definitely marked off from the cerebral lobes than these bodies are in the Yorkshire specimen.

COMPARISON OF THE PTERODACTYL SKULL WITH THOSE OF BIRDS AND LIZARDS.

The resemblances between Pterodactyls and Birds and Lizards have often been dwelt upon by writers on the Pterosauria; and it has been very generally agreed that these aberrant fossil creatures showed striking affinities to both these groups of living animals; but Professor SEELEY would assign them a position much nearer to Birds than most naturalists have been willing to allow, and in doing this he has laid great stress upon the characters of the brain deducible from the specimens alluded to above. The clearer light which *S. Purdoni* throws upon the structure of the Pterosaurian skull and brain lends a fresh interest to a renewed comparison with the two groups of the Sauropsida, and in some points strengthens Professor SEELEY'S position.

When the skulls of Birds and Lizards are compared they are found to have many

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* 'Amer. Journ. Sci.,' vol. 27, 1884, p. 423, and 'Geol Mag,' vol. 1, 1884, p 345

† 'Ornithosauria,' 1870, p 77.

‡ 'Ann Mag Nat. Hist' ser. 4, vol 7, p 20.

§ 'Linn Soc. Journ.,' vol 13, 1876, p. 84.

|| 'Geol. Soc Quart Journ,' vol 32, 1876, p. 496.

¶ 'Ornithosauria,' Plate 11, figs 1 and 2.

** *Loc cit.*, Plate 11, figs 1 and 2.

structures in common, and we are not surprised therefore to find that several of the characters presented by the Pterodactyl skull are found in both these groups; but it is obvious that, while such characters may be evidence of near affinity to the Sauropsida, they do not show to which of the two groups the Pterodactyls are most nearly related It is the characters which serve to distinguish between the skulls of Birds and Lizards which in the present instance will be of most service, and the more important of these will now be noticed.

1. The large size of the brain case, in proportion to the rest of the skull, in Birds, is one of their most marked characters when compared with Lizards.

2. The quadrate, pterygoid, and palatine bones are moveable on the skull in Birds, but more or less fixed in Lizards.

3. In Birds the hinder end of the palatine and front end of the pterygoid are brought into close relation with the rostrum of the sphenoid, and, in all but struthious Birds, are distinctly articulated with the rostrum. This is not the case with Lizards.

4. The orbit is rarely completed by bone in Birds, and when it is so completed it is not by the jugal bone. In Lizards the orbit is surrounded by bone, and the jugal forms part of it.

5. In Birds there is no pre-frontal bone, while it is always present in Lizards; but it may be noted that in some Birds, such as the Goose, the upper part of the nasal bone, where divided across by the "hinge," has much the appearance and occupies the position of a pre-frontal.

6. No Bird has the supra-temporal bar, which is always developed in Lizards.

7. The back of the skull in Lizards is characterised by a pair of large paroccipital processes, developed from the opisthotic bones, which run outwards and meet the post-temporal buttress and quadrate. In Birds there is no such bar, the paroccipital being short and formed chiefly by the exoccipital.

8. In Birds the bones of the cranium are early ankylosed, while in Lizards they nearly always remain separate.

9. In Birds the premaxillæ are large and united to form one bone, which sends backwards a long process (sometimes divided), nearly, if not quite, reaching the frontals. Lizards usually have the premaxillæ small, and there may be but one.

10. The ant-orbital fossa, which is present in Birds, is only occasionally indicated in Lizards (*Lyriocephalus, fide* OWEN), and is absent in some Pterodactyls.

11. In Birds there is a lower temporal bar of bone extending from the maxilla to the quadrate. This bar is not completed by bone in any Lizard except *Sphenodon*. However, other Reptiles have this lower bar as strongly developed as in Pterodactyls.

In the first seven of the above characters the skull of *Scaphognathus Purdoni* agrees with Lizards, and not with Birds.

In the characters numbered 8 and 9 *S. Purdoni* agrees with Birds, and not with Lizards.

The last two characters, numbered 10 and 11, being variable, afford no evidence of the affinities of Pterodactyls.

Comparison of the Pterodactyl Brain with those of Birds and Lizards.

In an upper or in a side view of the brain of a Reptile one sees behind the cerebral hemispheres a pair of more or less rounded optic lobes, and behind these again the single rounded cerebellum. This separation of the cerebrum from the cerebellum by the optic lobes occurs in all Reptiles, although the form and proportions of the parts may vary; thus in Chelonians the cerebrum is elongated, while in Alligators it is rounded and globose.

The most striking characteristic of a Bird's brain as compared with that of any Reptile is its much larger size in proportion to the bulk of the skull. The brain of a Bird seen from above seems, at first sight, to have no optic lobes, for directly behind the inflated cerebrum there is the cerebellum, the latter has, in fact, increased in size, and grown forwards between the optic lobes, which have thus been pressed outwards and downwards. At the same time the cerebrum has also enlarged, and, pressing backwards, has overlapped the optic lobes and shut them out from forming any part of the upper surface of the brain. In a side view, however, the optic lobe is seen as a rounded body quite at the lower part of the brain, and almost hidden by the cerebrum. Another peculiarity of the Bird's brain is the process from each side of the medulla, which occupies the fossa on the inner side of the periotic capsule, and is called the flocculus. I am not aware of this having been observed in Reptiles.

The brain of *Scaphognathus Purdoni*, it will be seen, agrees with that of the Reptile in its small size in proportion to the skull, in the relatively large size of the optic lobes, and in those bodies being placed behind the cerebrum on the upper surface of the brain. It is tolerably certain that the cerebellum intervened between the two optic lobes, and in this particular, therefore, the brain resembled that of the Bird and differed from that of the Reptile. At the side of this fossil brain the optic lobe extends from the upper to the lower surface; its presence on the upper surface is, as we have seen, a Reptilian character; and its presence as a rounded mass on the lower surface is an Avian character. The most important characters in which this Pterodactyl brain resembles that of a Bird is in the extension of the cerebellum between the optic lobes, in the possession of flocculi, and in the optic lobes forming rounded masses at the base of the brain.

The relations of these brains will, perhaps, be best appreciated by placing the characters in a tabular form, thus:—

Bird brain.	*S Purdoni* brain.	Reptile brain
1 Brain relatively large	1 Brain relatively small .	1 Brain relatively small
2 Cerebellum between optic lobes	2. Cerebellum between optic lobes	2 Cerebellum *not* between optic lobes, but behind them
3 Optic lobes at base	3 Optic lobes at base . .	3 Optic lobes *not* at base
4 Optic lobes *not* at top	4 Optic lobes at top . .	4 Optic lobes at top
5. Flocculi present	5 Flocculi present . . .	5 Flocculi *not* present

The Pterodactyl brain described by Professor SEELEY has already been alluded to, and I am not aware of any other fossil Reptile brain with which that of *S. Purdoni* could be profitably compared.

No comparison of the skull and brain of a Pterodactyl would be complete which did not take into account those remarkably Reptilian Birds the Archæopteryx and the toothed Birds of North America.

The skull of *Archæopteryx* has been described by Professor W. DAMES,* and Dr. H. WOODWARD has reproduced the enlarged figure of it.† The presence of teeth in the front of the jaw, and the distinct ant-orbital fossa completely separated from the orbit by a bony bar give to this skull a strong resemblance to that of a Pterosaurian. Unfortunately, the back of the head is broken; but, in so far as one can judge from the figures, it and the brain which it protected were relatively as large as in ordinary Birds On the slab containing the remains of *Archæopteryx*, in the British Museum, there is a "bilobed projection," which Dr. J. EVANS, no doubt correctly, described as a cast of part of the interior of the brain cavity;‡ but this is not sufficiently well preserved to allow of a comparison being made.

The skulls of *Hesperornis* and *Ichthyornis*, described by Professor MARSH,§ depart from the ordinary Avian type and approach Reptiles in the relatively small size of the brain case and in the possession of teeth; in these particulars they also resemble Pterosaurians; but in other particulars they conform to ordinary Bird characters.

Casts of the brain cavities of both *Hesperornis* and *Ichthyornis* have been described,‖ and these indicate a brain more like that of *S. Purdoni* than is that of any other Bird or Reptile with which I am acquainted. The two forms of toothed Birds have such similar brains that it will only be necessary here to speak of one of them. The relatively small size of the cranial cavity of *Hesperornis* is well shown by Professor MARSH's figures,¶ where the brain and skull of a Loon (*Colymbus torquatus*) are compared with those of *Hesperornis*, the great difference between them being the small size of the cerebrum in the latter, and as a consequence more of the optic lobes are seen on the upper surface, but at the same time the cerebellum extends forwards between the optic lobes, and reaches to the cerebrum.

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* 'Berlin, Palaeont. Abhandl.,' vol. 2, part 3, 1884, p. 119.

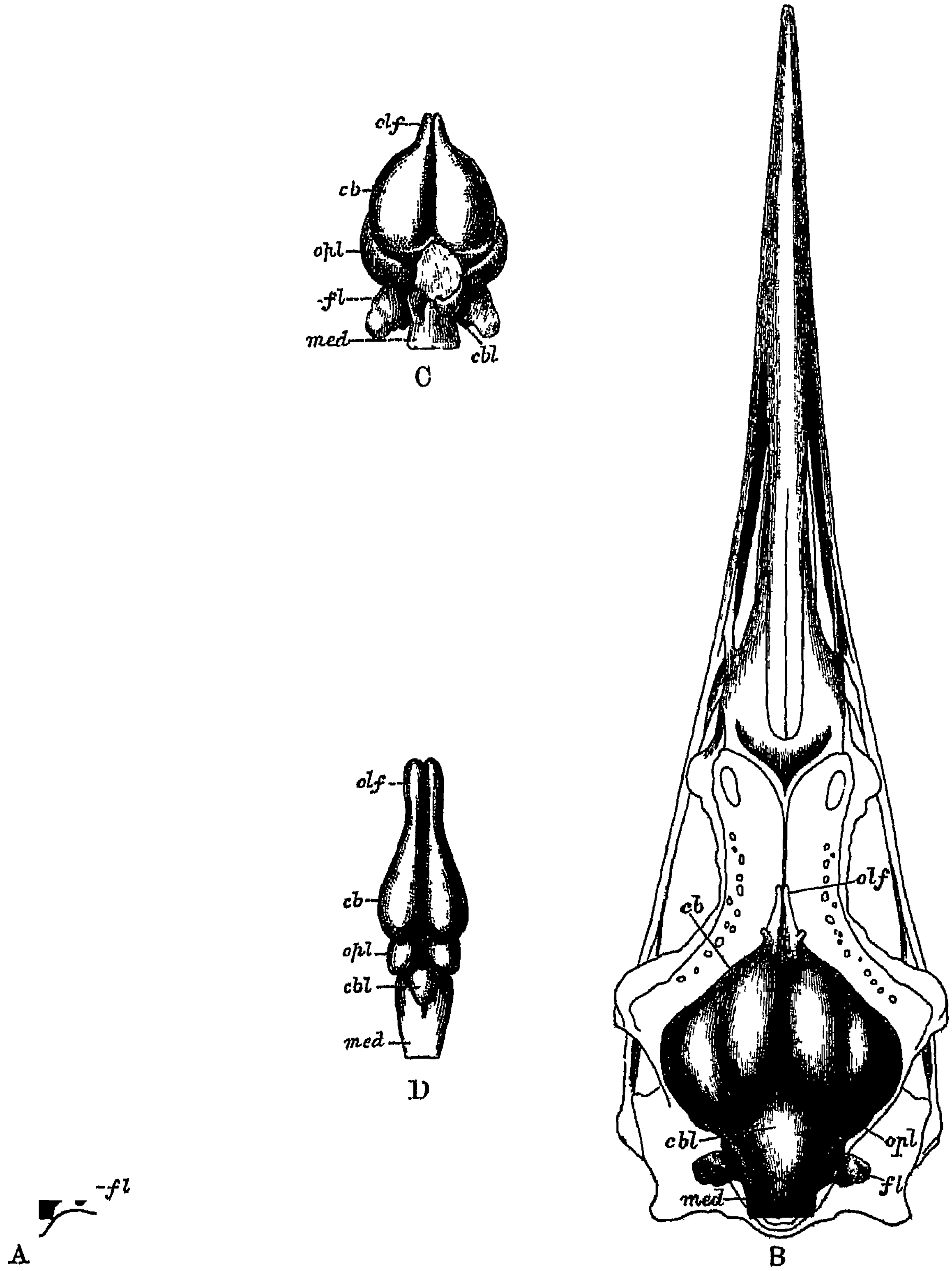
† 'Geol. Mag.,' vol. 1, 1884, pl 14, and 'Geol Assoc. Proc.,' vol. 9, 1886, p. 360.

‡ 'Nat. Hist. Rev.,' vol 5, 1865, p 415; reprinted with further remarks as a separate pamphlet, 8vo., London, 1881.

§ 'U.S. Geol. Expl 40th Parallel Report,' vol. 7, 1880, p. 9.

‖ *Loc. cit.*, pp. 9 and 122.

¶ *Loc. cit.*, p. 9.



A Skull and Brain of *Hesperornis*, three-fifths natural size (after MARSH).
B Skull and Brain of *Colymbus torquatus*, natural size (after MARSH).
C Brain of *Scaphognathus Purdoni*, natural size.
D. Brain of Lizard, enlarged.

A comparison of the figures will show more clearly than any words the close agreement between the brains of *Hesperornis* and *S. Purdoni*, but there are certain points of difference which must not be overlooked. In *Hesperornis* the brain is relatively larger, being about one-fifth of the length of the head, while in *S Purdoni* it is only about one-eighth. In the latter, also, the cerebellum is smaller, and the optic lobes larger, than in *Hesperornis*. Although the optic lobes of *Hesperornis* are well seen from above, yet they do not seem to reach the upper surface of the brain; while in *S. Purdoni* they form no inconsiderable part of the upper surface, and are as high as, if not higher than, the cerebrum itself.

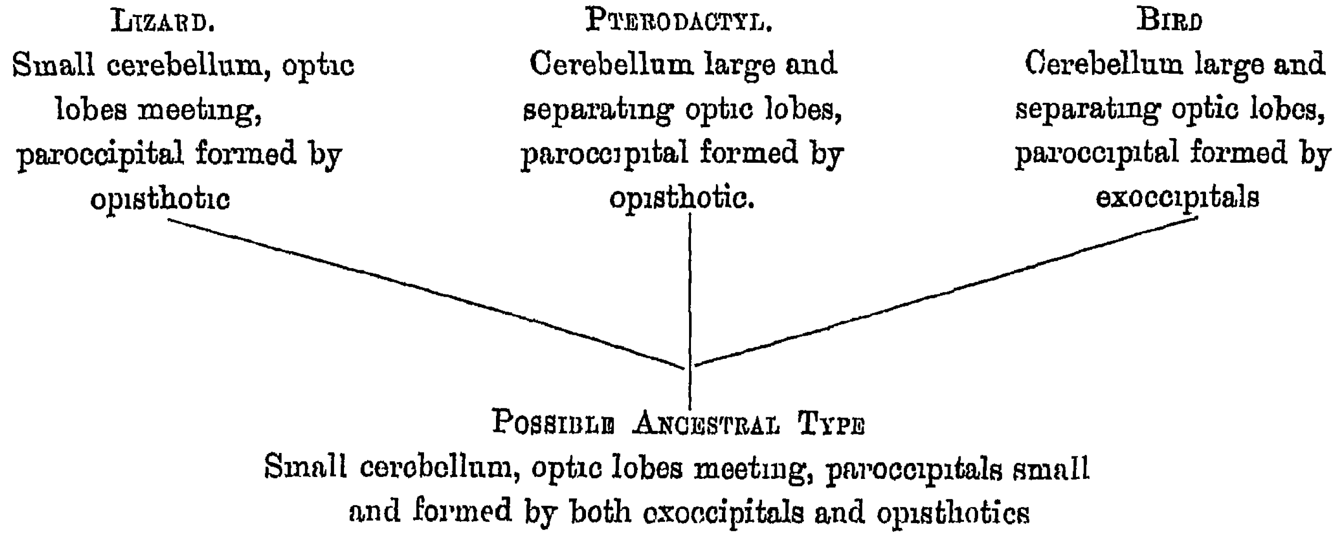
CONCLUSION.

The endeavour to trace the affinities of fossil animals is constantly leading us into unexpected difficulties and seeming incongruities. These difficulties, no doubt, arise sometimes from our want of knowledge, but often also from our inability to rightly interpret the known facts, which are only too frequently few in number, and serve rather to indicate the wide fields of knowledge yet to be searched than to furnish materials from which to draw definite conclusions. The organisation of the Pterosauria presents us with some of these difficulties.

The comparisons which have been made will, I think, make it clear that the Pterosaurian skull, as shown in *Scaphognathus Purdoni*, has a very close affinity to the skulls of Lacertilia in important points of structure, while the resemblances to the Avian skull are only superficial On the other hand, the brain of *S. Purdoni* departs from the Reptilian type, and makes an approach towards the brain of Birds, and more especially to the form found in the fossil *Hesperornis* and its allies. Accepting these facts, about which there can be no doubt, the Pterosauria show close affinities with both Birds and Reptiles From an evolutionist's point of view, this seems to be just what would be expected; and one is inclined to say at once, Here is the link connecting the two Sauropsidan groups. If Birds are modified and more highly developed Reptiles, the Pterodactyl was surely the intermediate stage, or, in other words, the Pterodactyl was the direct ancestor of the Bird. Is this really the case? I think not. The brain of *S. Purdoni* might, indeed, be taken as intermediate between that of Birds and of Reptiles, and it certainly makes such a near approach to the brain of *Hesperornis* that one cannot but recognise their close affinity.

With regard to the skull of *S. Purdoni*, however, it seems to me, it is as truly Reptilian as that of any Lizard living at the present day, and cannot therefore be said to be intermediate between Reptiles and Birds. It may be argued that all parts of an animal's organization would not necessarily change at the same time; but one modification would give rise to another. This is no doubt true, and it may be that the new development of the brain seen in the Pterodactyl subsequently caused modifications of the skull; but it must be remembered that, while the brain of *Hesperornis* is only a little more advanced than that of *S Purdoni*, the skull would seem, from Professor MARSH's description, to be that of a true Bird; and surely we ought to find the skull of the Pterodactyl more modified in the Avian direction if it were indeed an ancestor in the direct line of any Bird. The facts, as we at present know them, seem to point to Birds, Pterosauria, and Lizards having been derived from a common ancestor, possessing the general characters of all three, but with none of their specialisations.

If we take two or three of the characters of each of these forms as examples, the relationship may be put thus .—



LIZARD.
Small cerebellum, optic lobes meeting, paroccipital formed by opisthotic

PTERODACTYL.
Cerebellum large and separating optic lobes, paroccipital formed by opisthotic.

BIRD
Cerebellum large and separating optic lobes, paroccipital formed by exoccipitals

POSSIBLE ANCESTRAL TYPE
Small cerebellum, optic lobes meeting, paroccipitals small and formed by both exoccipitals and opisthotics

EXPLANATION OF PLATES 77 AND 78.

(All the figures natural size except No. 12)

Fig. 1 (Plate 77). *Scaphognathus Purdoni*, skull seen from above.
Fig. 2 (Plate 78). „ „ „ left side.
Fig. 3 (Plate 78). „ „ „ right side
Fig. 3*a* (Plate 78). „ „ „ side view of base and cranium.
Fig. 4 (Plate 77). „ „ „ palatal view.
Fig 5 (Plate 78). „ „ „ viewed from behind.
Fig. 6 (Plate 78). „ „ brain cast seen from left side.
Fig. 7 (Plate 78). „ „ „ from above and behind. The right side is only partly exposed in the fossil.
Fig. 8 (Plate 77). Skull of *Sphenodon punctata*, from above.
Fig. 9 (Plate 77). „ „ „ from below.
Fig. 10 (Plate 78). „ „ „ back view.
Fig. 11 (Plate 78). „ „ „ from right side.
Fig. 12 (Plate 78). Skull of young Fowl, back view (after PARKER).
Fig. 13 (Plate 77). „ *Dromæus Novæ Hollandiæ*, palatal view.

ant.orb.	Ant-orbital fossa.
ant.sc.	Anterior vertical semicircular canal.
b.o.	Basi-occipital.
b.p.p.	Basi-pterygoid process.
b.s.	Basi-sphenoid.
bt.	Basi-temporal
cb.	Cerebrum.
cbl.	Cerebellum.
en.	External nares.
ex.o.	Ex-occipital
fr.	Frontal bone.
fl.	Flocculus.
f.o.	Fenestra ovalis.
in.	Internal nares.
inf.tem.	Infra-temporal fossa.
ju.	Jugal.
la.	Lachrymal.
med.	Medulla oblongata.
mx.	Maxilla.
na.	Nasal bone.
olf.	Olfactory lobe of brain.
op.l.	Optic lobe.
op.ot.	Opisthotic.
orb.	Orbit.
pa	Parietal.
p.fr.	Pre-frontal.
pl.	Palatine.
pmx.	Premaxilla.
pt.	Pterygoid.
pt.fos.	Post-temporal fossa.
pt fr.	Post-frontal.
pt.o.	Post-orbital bone.
pt.sc.	Posterior vertical semicircular canal.
qu.	Quadrate.
qu.ju.	Quadrato-jugal.
so.	Supra-occipital.
sq.	Squamosal.
st.	Supra-temporal bone.
stp.	Stapes.
sup.tem.	Supra-temporal fossa.
vo.	Vomer.

APPENDIX I

CATALOGUE OF THE GENERA AND SPECIES OF ORNITHOSAURIA.

In bringing together all the generic and specific names that have been given to Ornithosaurians, I have been able to consult with Mr. R. LYDEKKER, F.G S., so that the synonymy here given may agree with the 'Catalogue of Fossil Reptiles in the British Museum,' which is now passing through the press

Full synonymy of the species previous to the year 1860 will be found in Professor HERMANN VON MEYER's 'Fauna der Vorwelt.'

	Brachytrachelus, Giebel	See SCAPHOGNATHUS
	Cimoliornis diomedeus, Owen	See ORNITHOCHEIRUS.
	Coloborhynchus, Owen	See ORNITHOCHEIRUS
	Cretornis, Fritsch	See ORNITHOCHEIRUS.
	Criorhynchus, Owen	See ORNITHOCHEIRUS
	CYCNORHAMPHUS SUEVICUS, Quenstedt.	(Lithographic Slate, Nusplingen, Würtemberg)
1854.	*Pterodactylus Wurttembergicus*	Quenstedt Neues Jahrb Mineral., p 570
		(This was not intended as a specific name. See 'Der Jura,' p 812.)
1855.	*Pterodactylus Suevicus*	Quenstedt 'Ueber Pterodactylus Suevicus, &c.' Tubingen, 1855
1860	„ *Wurttembergicus*	v. Meyer, 'Fauna d Vorwelt, Rept Lithog Schief,' p 50.
1861	„ *Suevicus*, subsp. *eurycheirus*	Wagner, Munchen, Bayer Akad. Sitzber., vol. 1, p 532.
		(Wagner also includes *P grandipelvis* as a subspecies.)
1870.	*Cycnorhamphus* „	Seeley, 'Ornithosauria,' p 111 (8vo., Cambridge).
1871.	„ „	Seeley, Ann Mag. Nat. Hist, ser 4, vol. 7, p. 20.
1878.	*Pterodactylus* „	Fraas, Palæontographica, vol. 25, p. 163
1882	„ „	Zittel, *ibid*, vol 29, p 80.
	DERMODACTYLUS MONTANUS, Marsh.	(Jurassic, Wyoming.)
1878	*Pterodactylus Montanus*	Marsh, Amer. Journ Sci., ser. 3, vol 16, p 233
1881	*Dermodactylus* „	Marsh, *ibid*, vol 21, p 342.
	Dimorphodon Banthensis, Theodori	See DORYGNATHUS
	DIMORPHODON MACRONYX, Buckland	(Lias, Lyme Regis.)
1829	*Pterodactylus macronyx*	Buckland, Geol. Soc Proc., Feb. 6, vol. 1, p. 96
1835	„ „	Buckland, Geol Soc. Trans, ser 2, vol. 3, p. 217.
1836.	„ „	Buckland, Bridgewater Treatise, pp. 221, 226.
1858.	*Dimorphodon* „	Owen, Brit. Assoc. Rep, 1858 (*Sect.*), p. 97
1859.	„ „	Owen, Phil. Trans, vol 149, p 161.
1860	*Rhamphorhynchus* „	v. Meyer, 'Fauna d Vorwelt, Rept. Lithog. Schief.,' p. 85.
1870.	*Dimorphodon* „	Owen, Pal. Soc for 1869, Lias Rept.
1870.	„ „	Seeley, Ann. Mag. Nat. Hist, ser. 4, vol. 6, p. 129.
1874.	„ „	Owen, Pal. Soc., Lias Rept., p. 13.
1874.	? *Pterodactylus Marderi*	Owen, Pal. Soc, Mesoz. Rept., p. 37.

	Diopecephalus, Seeley	See PTERODACTYLUS
		(Professor Seeley included in DIOPECEPHALUS *P longicollum*, *P rhamphastinus*, and *P Kochi*, Ann. Mag Nat Hist, vol 7, 1871, p 35, foot-note)
	Dolichorhamphus, Seeley .	See RHAMPHOCEPHALUS PRESTWICHI
	Doratorhynchus validus, Seeley .	See ORNITHOCHEIRUS.
	DORYGNATHUS BANTHENSIS, Theodori .	(Lias, Banz, near Boll, Wurtemberg)
1830	*Ornithocephalus Banthensis*	Theodori, Froriep's Notizen, No. 623, and Isis, 1831, col 276
1831	*Pterodactylus macronyx*	v Meyer, Nova Acta Leopold, vol. 15, pt 2, p. 198.
1852	*Rhamphorhynchus Banthensis*	Theodori, Bamberg Naturf. Ver. Bericht, p 17.
1858.	,, ,,	Wagner, Munchen, Bayer Akad Sitzber., vol. 8, pt 2, p 502
1860.	,, *macronyx* .	v Meyer (in part), 'Fauna d. Vorw., Rept Lith. Schief,' p. 85.
1860.	*Dorygnathus Banthensis*	Wagner, Munchen, Bayer Akad Sitzber., p 48
1861	,, ,,	Wagner, *ibid*, vol. 1, p. 520
1882.	,, ...	Zittel, Palæontographica, vol 29, p. 64
	? *Pterodactylus Goldfussi* .	Theodori, 1830 (*fide* Bronn, 'Index Palæont.,' p. 1082).
	Macrotrachelus, Giebel	See PTERODACTYLUS.
	NYCTODACTYLUS GRACILIS, Marsh . .	(Cretaceous, Kansas.)
1876.	*Pteranodon gracilis*	Marsh, Amer. Journ. Sci., ser. 3, vol. 11, p. 508
1876.	*Nyctosaurus gracilis* . .	Marsh, *ibid.*, vol 12, p. 479.
1881.	*Nyctodactylus gracilis* . . .	Marsh, *ibid*, vol. 21, p. 342, note.
	Nyctosaurus, Marsh	See NYCTODACTYLUS.
	Ornithocephalus, Soemmerring	See PTERODACTYLUS and RHAMPHORHYNCHUS.
	ORNITHOCHEIRUS BRACHYRHINUS, Seeley . .	(Cambridge Greensand.)
1870	*Ornithocheirus brachyrhinus* . .	Seeley, 'Ornithosauria,' p. 123.
	ORNITHOCHEIRUS BÜNZELI, Seeley	(? Upper Greensand, Gosau, near Vienna.)
1881.	*Ornithocheirus Bunzeli* . . .	Seeley, Geol. Soc Quart. Journ., vol. 37, p. 701.
1882.	,, ,, . . .	Sauvage, Soc. Géol. France Mém., ser. 3, vol. 2, p. 1.
	ORNITHOCHEIRUS CAPITO, Seeley	(Cambridge Greensand.)
1870.	*Ornithocheirus capito* . . .	Seeley, 'Ornithosauria,' p. 126.
	ORNITHOCHEIRUS CARTERI, Seeley . .	(Cambridge Greensand.)
1870	*Ornithocheirus Carteri* .	Seeley, 'Ornithosauria,' p. 128.
	ORNITHOCHEIRUS CLAVIROSTRIS, Owen . .	(Wealden, St Leonards)
1874.	*Coloborhynchus clavirostris* .	Owen, Pal. Soc, Mesoz. Rept., p. 6.
	ORNITHOCHEIRUS CLIFTI, Mantell .	(Wealden, Hastings.)
1827	Bones of Birds . . .	Mantell, 'Fossils of Tilgate Forest,' p. 81.
1840.	,, ,, ...	Mantell, Geol Soc Trans, ser. 2, vol. 5, p. 175.
1844.	*Palæornis Clifti*	Mantell, 'Medals of Creation,' p. 806.
1846.	*Pterodactylus*	Owen, Geol. Soc. Quart. Journ., vol. 2, p. 96.
1846	Fossil Remains of Birds .	Mantell, *ibid*, p. 104
1848.	*Pterodactylus Clifti*	Bronn, 'Index Palæont.,' p. 895.
1854.	,, ...	Morris, 'Cat. Brit. Foss.,' p. 353.
	ORNITHOCHEIRUS COLORHINUS, Seeley	(Cambridge Greensand.)
1870.	*Ornithocheirus colorhinus* . .	Seeley, 'Ornithosauria,' p. 124.

Ornithocheirus compressirostris, Owen		(Lower Chalk, Burham, Greensand, Maidstone, Wealden, Tilgate, and Portland, Solothurn, Switzerland)
1851	*Pterodactylus compressirostris*	Owen, Zool Soc Proc, 1851, p 32
1851	„ „	Owen, Pal. Soc, Cret Rept., pp. 95, 98
1858	„ „	Wagner, Munchen, Bayer Akad Abhandl, vol 8, pt 2, p 497
1878	„ „	Owen, Dixon's 'Foss Sussex,' edit 2, p. 428.
Ornithocheirus crassidens, Seeley		(Cambridge Greensand)
1870.	*Ornithocheirus crassidens*	Seeley, 'Ornithosauria,' p. 122
Ornithocheirus ? curtus, Owen		(Wealden, Sussex.)
1870	*Pterodactylus curtus*	Owen, Pal. Soc, Lias Rept, pt 2, pl 19, figs 8, 9
Ornithocheirus Cuvieri, Bowerbank		(Lower Chalk, Burham, Cambridge Greensand)
1840.	Remains of Bird	Owen, Geol Soc Proc, vol 3, p 298
1842	„ „	Owen, Geol Soc. Trans, ser 2, vol 6, pt 2, p 411
1851	*Pterodactylus Cuvieri*	Bowerbank, Zool Soc Proc, p 14
1851	„ „	Owen, Pal Soc, Cret Rept, pp. 88, 97
1858.	„ „	Wagner, Munchen, Bayer Akad Abhandl, vol 8, pt 2, p 497
1861	„ „	Owen, Pal. Soc., Cret Rept, suppl. iii, pl. 3, figs 1–3
1870	*Ornithocheirus* „	Seeley, 'Ornithosauria,' p. 113.
1874.	*Coloborhynchus* „	Owen, Pal Soc, Mesoz Rept., pt 1, p. 6
1878.	*Pterodactylus* „	Owen, Dixon's 'Foss Sussex,' p 428
Ornithocheirus Daviesi, Owen		(Gault, Folkestone)
1874.	*Pterodactylus Daviesi*	Owen, Pal. Soc., Mesoz. Rept, pt 1, p. 2
Ornithocheirus dentatus, Seeley		(Cambridge Greensand)
1870	*Ornithocheirus dentatus*	Seeley, 'Ornithosauria,' p 119
Ornithocheirus denticulatus, Seeley		(Cambridge Greensand)
1870.	*Ornithocheirus denticulatus*	Seeley, 'Ornithosauria,' p 122.
Ornithocheirus diomedeus, Owen		(Chalk, Kent.)
1840	Bird allied to Albatross	Owen, Geol. Soc Trans., ser 2, vol. 6, p 411
1846.	*Cimolornis diomedeus*	Owen, 'Brit Foss Mam and Birds,' p 545
1851.	*Pterodactylus* „	Owen, Zool Soc. Proc, p 28
1851.	Large Pterodactyle	Owen, Pal Soc, Cret Rept, p 192, pl 32, figs 4, 5
1854	*Pterodactylus giganteus*	Morris, 'Cat Brit Foss,' p 353
		(All the above refer to the same specimen, which may be identical with *O giganteus*)
Ornithocheirus enchorhynchus, Seeley		(Cambridge Greensand)
1870	*Ornithocheirus enchorhynchus*	Seeley, 'Ornithosauria,' p. 123.
Ornithocheirus eurygnathus, Seeley		(Cambridge Greensand.)
1870	*Ornithocheirus eurygnathus*	Seeley, 'Ornithosauria,' p. 123.
Ornithocheirus Fittoni, Owen		(Cambridge Greensand)
1858	*Pterodactylus Fittoni*	Owen, Brit. Assoc. Rep., 1858 (*Sect.*), p 98.
1859	„ „	Owen, Pal. Soc, Cret. Rept. sup. 1, p 4
1859.	„ „	Owen, Phil Trans, vol. 149, p 161
1870.	*Ornithocheirus Fittoni*	Seeley, 'Ornithosauria,' p 118
Ornithocheirus giganteus, Bowerbank		(Upper Chalk, Kent)
1846	*Pterodactylus giganteus*	Bowerbank, Geol Soc. Quart Journ, vol 2, p. 7
		(Paper read May 14, 1845; species named in note dated December, 1845.)
1848.	„ „	Bowerbank, *ibid.*, vol. 4, p. 2.

1850 *Pterodactylus conirostris*	Owen, Dixon's 'Foss. Sussex,' 1st edit, p 401.
1851 " *giganteus*	Bowerbank, Zool Soc. Proc, p 14.
1851 " "	Owen, Pal Soc, Cret Rept p 91.
1858 " *conirostris*	Wagner, Munchen, Bayer Akad Abhandl, vol 8, pt 2, p 497
1878 " *giganteus*	Owen, Dixon's 'Foss Sussex,' edit 2, p 427
Ornithocheirus harpyia, Cope	See PTERANODON OCCIDENTALIS
ORNITHOCHEIRUS HILSENSIS, Koken	(Neocomian, Hils, Hanover)
1883 *Ornithocheirus Hilsensis*	Deutsch Geol. Gesell Zeitschr, vol 35, p 824, and vol 37, 1885, p. 214
	(Referred to *Dinosaur* by Otto Meyer, Deutsch Geol Gesell Zeitschr, vol 36, 1884, p 664, and by S W Williston, Zool. Anzeig, vol. 8, 1885, p 628)
ORNITHOCHEIRUS HLAVATSCHI, Fritsch.	(Upper Chalk, Bohemia)
1881 *Cretornis Hlavatschi*.	Fritsch, Prag, Bohm. Gesell Sitzber, 1880, p 276
1888 *Ornithocheirus* "	Lydekker, 'Cat Foss Rept Brit Mus,' p 14.
ORNITHOCHEIRUS HUXLEYI, Seeley	(Cambridge Greensand)
1870. *Ornithocheirus Huxleyi*.	Seeley, 'Ornithosauria,' p. 116
ORNITHOCHEIRUS MACHÆRORHYNCHUS, Seeley.	(Cambridge Greensand.)
1870. *Ornithocheirus machærorhynchus*	Seeley, 'Ornithosauria,' p 113
ORNITHOCHEIRUS MICRODON, Seeley.	(Cambridge Greensand.)
1870. *Ornithocheirus microdon*	Seeley, 'Ornithosauria,' p. 116
ORNITHOCHEIRUS NASUTUS, Seeley	(Cambridge Greensand.)
1870. *Ornithocheirus nasutus*	Seeley, 'Ornithosauria,' p 120.
ORNITHOCHEIRUS NOBILIS, Owen.	(Wealden, Isle of Wight.)
1870 *Pterodactylus nobilis*	Owen, Pal Soc., Lias Rept, pt 2, pl. 19, fig 10
ORNITHOCHEIRUS OWENI, Seeley	(Cambridge Greensand)
1870 *Ornithocheirus Oweni*	Seeley, 'Ornithosauria,' p 115
ORNITHOCHEIRUS OXYRHINUS, Seeley	(Cambridge Greensand.)
1870. *Ornithocheirus oxyrhinus*.	Seeley, 'Ornithosauria,' p. 117.
ORNITHOCHEIRUS PLATYRHINUS, Seeley	(Cambridge Greensand.)
1870. *Ornithocheirus platyrhinus*	Seeley, 'Ornithosauria,' p. 128
ORNITHOCHEIRUS PLATYSOMUS, Seeley.	(Cambridge Greensand)
1870 *Ornithocheirus platysomus*	Seeley, 'Ornithosauria,' p 120
ORNITHOCHEIRUS POLYODON, Seeley	(Cambridge Greensand.)
1870 *Ornithocheirus polyodon*	Seeley, 'Ornithosauria,' p 121
ORNITHOCHEIRUS REEDII, Seeley	(Cambridge Greensand.)
1870. *Ornithocheirus Reedii*	Seeley, 'Ornithosauria,' p. 126
1881 " "	Seeley, Geol Mag, Dec 2, vol. 8, p. 3
ORNITHOCHEIRUS SAGITTIROSTRIS, Owen	(Wealden, St. Leonards)
1874. *Pterodactylus sagittirostris*	Owen, Pal. Soc., Mesoz. Rept., pt. 1, p. 3.
ORNITHOCHEIRUS SCAPHORHYNCHUS, Seeley	(Cambridge Greensand)
1870 *Ornithocheirus scaphorhynchus*	Seeley, 'Ornithosauria,' p. 119.
ORNITHOCHEIRUS SEDGWICKII, Owen	(Cambridge Greensand.)
1858. *Pterodactylus Sedgwickii*	Owen, Brit. Assoc. Rep., 1858 (*Sect.*), p. 98
1859. [illegible]	Owen, Pal Soc, Cret. Rept, suppl. 1, p 2.
1859. [illegible]	Owen, Phil. Trans., vol 149, p. 161.

1860.	*Ptenodactylus Sedgwickii*	Owen, 'Palæontology,' p 427
1870	*Ornithocheirus* ,,	Seeley, 'Ornithosauria,' p 112
1874	*Coloborhynchus* ,,	Owen, Pal Soc, Mesoz Rept, pt 1, p 6
1882.	? *Ornithocheirus*	Sauvage, Soc Géol France Mém, ser 3, vol. 2, pt. 4, p. 6
ORNITHOCHEIRUS SIMUS, Owen		(Cambridge Greensand)
1861	*Pterodactylus simus*	Owen, Pal Soc, Cret. Rept, suppl 3, p. 2
1870	*Ornithocheirus* ,,	Seeley, 'Ornithosauria,' p 127.
1874	*Criorhynchus* ,,	Owen, Pal Soc, Mesoz Rept, pt 1, p 7
		(*Pterodactylus Woodwardi*, Owen, may belong to this species)
ORNITHOCHEIRUS TENUIROSTRIS, Seeley		(Cambridge Greensand)
1870	*Ornithocheirus tenuirostris*	Seeley, 'Ornithosauria,' p 114
Ornithocheirus umbrosus, Cope		See PTERANODON INGENS
ORNITHOCHEIRUS ? VALIDUS, Owen		(Purbeck, Swanage)
1869	*Pterodactylus macrurus*	Seeley, 'Index to Aves, Ornithosauria, &c,' Cambridge, p 89
1870.	,, *validus*	Owen, Pal Soc, Lias Rept, pt 2, pl. 19, fig 7
1875	*Doratorhynchus validus*	Seeley, Geol Soc Quart Journ., vol 31, p 465
ORNITHOCHEIRUS WOODWARDI, Owen		(Cambridge Greensand)
1861	*Pterodactylus Woodwardi*	Owen, Pal Soc., Cret. Rept, suppl 3, p 4
1870	*Ornithocheirus* ,,	Seeley, 'Ornithosauria,' p. 125.
		(This species may be identical with *O simus*)
ORNITHOCHEIRUS XYPHORHYNCHUS, Seeley		(Cambridge Greensand)
1870.	*Ornithocheirus xyphorhynchus*	Seeley, 'Ornithosauria,' p. 117
1881	,, ,,	Seeley, Geol Mag, Dec 2, vol. 8, p. 18
ORNITHOPTERUS LAVATERI, v. Meyer		(Lithographic Slate, Bavaria)
1837	*Pterodactylus*	v Meyer, Neues Jahrb. Mineral, p 558
1838	,, *Lavateri*	v Meyer, *ibid*, p 415
1860	*Ornithopterus* ,,	v. Meyer, 'Fauna d. Vorwelt, Rept Lithog Schief,' p 25
ORNITHOSTOMA, Seeley		(Cambridge Greensand)
1871	*Ornithostoma*	Ann Mag Nat Hist, ser 4, vol 7, p 35, note
		(The portions of jaws thus named may perhaps belong to *Ornithocheirus*.)
Palæornis, Mantell		See ORNITHOCHEIRUS CLIFTI
Pachyrhamphus, Fitzinger		See SCAPHOGNATHUS
Ptenodactylus, Seeley		See ORNITHOCHEIRUS
		(See 'Index to the Fossil Remains of Aves, Ornithosauria, &c, in the Woodwardian Museum,' 8vo, Cambridge, 1869, p xvi)
PTENODRACON BREVIROSTRIS, Soemmerring		(Lithographic Slate, Eichstatt, Bavaria)
1816–17.	*Ornithocephalus brevirostris*	Soemmerring, Munchen, Bayer Akad Denksch, vol 6, p 89
1826.	*Pterodactylus nettecephaloides*	Ritgen, Nova Acta Leopold, vol 13, pt 1, p 338
1842.	,, *Meyeri*	Munster, Neues Jahrb Mineral, p 35
1860	,, *brevirostris*	v Meyer, 'Fauna d. Vorwelt, Rept Lithog. Schief.,' p. 55
1860.	,, *Meyeri*	v. Meyer, *ibid*, p. 56.
1861.	,, *brevirostris*	Wagner, Munchen, Bayer Akad. Sitzber, vol. 1, p. 533
1861	,, *Meyeri*	Wagner, *ibid*, p 533.
1870	*Ornithocephalus brevirostris*	Seeley, 'Ornithosauria,' p. 111
1882	*Pterodactylus* ,,	Zittel, Palæontographica, vol 29, p 78
1888.	*Ptenodracon* ,,	Lydekker, 'Cat. Foss Rept. Brit Mus,' p 3.

PTERANODON COMPTUS, Marsh		(Cretaceous, Kansas.)
1876	*Pteranodon comptus*	Marsh, Amer Journ. Sci, ser 3, vol. 11, p 509
1876	,, ,,	Marsh, *ibid*, vol 12, p. 479
Pteranodon gracilis, Marsh		See NYCTODACTYLUS
PTERANODON INGENS, Marsh		(Cretaceous, Kansas.)
1872	*Pterodactylus ingens*	Marsh, Amer Journ Sci, ser. 3, vol 3, p 246
1872	*Ornithocheirus umbrosus*	Cope, Amer. Phil Soc Proc., vol 12, p 421
1875	,, ,,	Cope, U S. Geol. Surv Terr, vol 2, pp 65 and 249
1876	*Pteranodon ingens*	Marsh, Amer Journ Sci, ser 3, vol. 11, p. 507, vol 12, p 479; also vol. 27, 1884, p 423; and Geol. Mag, vol. 1, 1884, p 345.
PTERANODON LONGICEPS, Marsh		(Cretaceous, Kansas)
1876	*Pteranodon longiceps*	Marsh, Amer Journ. Sci, ser. 3, vol. 11, p 508, vol. 12, 1876, p 479, vol 27, 1884, p 423, and Geol Mag, vol. 1, 1884, p 345
PTERANODON NANUS, Marsh		(Cretaceous, Kansas)
1881.	*Pteranodon nanus*	Marsh, Amer Journ. Sci, ser. 3, vol 21, p. 343.
PTERANODON OCCIDENTALIS, Marsh		(Cretaceous, Kansas)
1871.	*Pterodactylus Oweni*	Marsh, Amer. Journ Sci., ser. 3, vol 1, p 472.
1872.	,, *occidentalis*	Marsh, *ibid.*, vol. 3, p 241.
1872.	*Ornithocheirus harpyia*	Cope, Amer Phil Soc. Proc., vol. 12, p 421.
1875	*Pterodactylus occidentalis*	Cope, U.S. Geol Surv. Terr., vol 2, pp. 66 and 249.
1876.	*Pteranodon* ,,	Marsh, Amer Journ. Sci., ser. 3, vol. 12, p 479; also Amer Journ. Sci, ser 3, vol. 27, 1884, p. 423; and Geol Mag, vol. 1, 1884, p. 345
	Non *Ornithocheirus Oweni*	Seeley
PTERANODON VELOX, Marsh		(Cretaceous, Kansas)
1872.	*Pterodactylus velox*	Marsh, Amer. Journ Sci, ser 3, vol. 3, p 247
1875.	,, ,,	Cope, U.S. Geol. Surv. Terr., vol. 2, p. 250.
1876	*Pteranodon* ,,	Marsh, Amer Journ. Sci., vol. 11, p 507; and vol. 12, p. 479.
Pterodactylus Aclandi, Owen		See RHAMPHOCEPHALUS DEPRESSIROSTRIS.
PTERODACTYLUS ANTIQUUS, Soemmerring		(Lithographic Slate, Pappenheim, Bavaria)
1784	"Un genre particulier"	Collini, Mannheim, Acad. Theod. Palat. Acta, vol 5, p. 58.
1812	*Ornithocephalus antiquus*	Soemmerring, Munchen, Bayer. Akad. Denksch., vol. 3, p. 126
1824	*Pterodactylus longirostris*	Cuvier, Oss Foss., vol 5, pt 2, p. 359.
1826.	,, *crocodilocephaloides*	Ritgen, Nova Acta Leopold, vol. 13, pt 1, p. 344.
1860.	,, *longirostris*	v Meyer, 'Fauna d. Vorwelt, Rept. Lithog. Schief,' p 26.
1861.	,, ,,	Wagner, Munchen, Bayer. Akad Sitzber., vol 1, p 532 (Wagner also includes *P. scolopaciceps* as a subspecies of *P longirostris*)
Pterodactylus Banthensis, Theodori		See DORYGNATHUS.
Pterodactylus brevirostris, Soemmerring		See PTENODRACON.
Pterodactylus Bucklandi, v. Meyer		See RHAMPHOCEPHALUS.
PTERODACTYLUS CIRINENSIS, v. Meyer		(Lithographic Slate, Cirin, E. France.)
1852.	*Pterodactylus*	v Meyer, Neues Jahrb Mineral., p. 832.
1860.	,, *Cirinensis*	v Meyer, 'Fauna d. Vorwelt, Rept. Lithog Schief,' p 66.
1861.	,, ,,	Wagner, München, Bayer Akad. Sitzber., vol. 1, p. 525

	Pterodactylus Clifti, Owen	See Ornithocheirus
	Pterodactylus compressirostris, Owen	See Ornithocheirus
	Pterodactylus conirostris, Owen	See Ornithocheirus giganteus
	Pterodactylus crassipes, Meyer	(Lithographic Slate, Eichstatt, Bavaria)
1857	*P. (Rhamphorhynchus) crassipes*	v. Meyer, Neues Jahrb. Mineral., p. 535
1860.	*Pterodactylus* „	v. Meyer, 'Fauna d. Vorwelt, Rept. Lithog. Schief.,' p. 64
1861	*Scaphognathus* „	Wagner, as var. of *S. crassirostris*, Munchen, Bayer. Akad. Sitzber., vol. 1, p. 524
	Pterodactylus crassirostris, Goldfuss	See Scaphognathus
	Pterodactylus crocodilocephaloides, Ritgen	See Pterodactylus antiquus
	Pterodactylus curtus, Owen	See Ornithocheirus
	Pterodactylus Cuvieri, Bowerbank	See Ornithocheirus
	Pterodactylus Daviesi, Owen	See Ornithocheirus.
	Pterodactylus dubius, Münster	(Lithographic Slate, Bavaria)
1832	*Pterodactylus*, new species	Münster, Neues Jahrb. Mineral., p. 412.
1843	*Pterodactylus dubius*, Münster	v. Meyer, Neues Jahrb. Mineral., p. 584
1851.	*Ornithocephalus dubius*	Wagner, München, Bayer. Akad. Abhandl., vol. 6, pt. 1, p. 148
1860.	*Pterodactylus* „	v. Meyer, 'Fauna d. Vorwelt, Rept. Lithog. Schief.,' p. 52
1861.	„ „	Wagner, as sub-species of *P. rhamphastinus*, Munchen, Bayer. Akad. Sitzber., vol. 1, p. 531
	Pterodactylus Duncani, Owen	See Rhamphocephalus Bucklandi.
	Pterodactylus elegans, Wagner	(Lithographic Slate)
1860	*Pterodactylus longirostris*	v. Meyer, 'Fauna d. Vorwelt, Rept. Lithog. Schief.,' pl. 1, fig. 1
1861	„ *pulchellus*	v. Meyer, Neues Jahrb. Mineral., p. 470
1861	„ „	v. Meyer, Palæontographica, vol. 10, p. 9.
1861	„ *elegans*	Wagner, Munchen, Bayer. Akad. Sitzber., vol. 1, pp. 363, 533.
1882.	„ „	Zittel, Palæontographica, vol. 29, pp. 50, 73.
	Pterodactylus eurycheirus, Wagner	See Cycnorhamphus Suevicus.
	Pterodactylus Fittoni, Owen	See Ornithocheirus.
	Pterodactylus Gemmingi, v. Meyer	See Rhamphorhynchus
	Pterodactylus giganteus, Bowerbank	See Ornithocheirus
	Pterodactylus Goldfussi, Theodori	See Dorygnathus Banthensis.
	Pterodactylus gracilis, Theodori	(Lithographic Slate)
1852.	*Pterodactylus gracilis*	Theodori (*fide* v. Meyer).
1860.	„ „	v. Meyer, 'Fauna d. Vorwelt, Rept. Lithog. Schief.,' p. 7
	Pterodactylus grandipelvis, v. Meyer	(Lithographic Slate, Eichstätt, Bavaria)
1860.	*Pterodactylus grandipelvis*	v. Meyer, 'Fauna d. Vorwelt, Rept. Lithog. Schief.,' p. 53
1865.	„ „	v. Meyer, Neues Jahrb. Mineral., p. 845.
1861.	„ „	Wagner, as subspecies of *P. Suevicus*, Munchen, Bayer. Akad., Sitzber., vol. 1, p. 524
	Pterodactylus grandis, Cuvier	See Rhamphorhynchus.
	Pterodactylus hirundinaceus, Wagner	See Rhamphorhynchus Münsteri.
	Pterodactylus Hopkinsi, Seeley	

(This name, with others, was given for specimens from the Cambridge Greensand, Brit. Assoc. Rep., 1864 (*Sect.*), p. 69, but has not since been used.)

Pterodactylus ingens, Marsh		See PTERANODON
Pterodactylus intermedius, Goldfuss .		See PTERODACTYLUS MEDIUS
Pterodactylus Kiddi, Owen .		See RHAMPHOCEPHALUS BUCKLANDI
PTERODACTYLUS KOCHI, Wagner .		(Lithographic Slate, Kelheim and Eichstätt, Bavaria.)
1831–6	*Ornithocephalus Kochi* . .	Wagner, Munchen, Bayer Akad Abhandl., vol 2, p 168.
1850	*Pterodactylus scolopaciceps* . .	v Meyer, Neues Jahrb Mineral., p 199
1860	„ *Kochi* . .	v Meyer, 'Fauna d. Vorwelt, Rept. Lithog. Schief,' p 35
1860	„ *scolopaciceps* .	v. Meyer, *ibid.*, p 33
1861	„ „ .	Wagner, Munchen, Bayer Akad. Sitzber., vol 1, pp. 522 and 532
1861	„ *Kochi* .	Wagner, *ibid.*, vol. 1, p 533.
1871	*Diopecephalus* „	Seeley, Ann. Mag Nat. Hist., ser. 4, vol 7, p 35, note
1882	*Pterodactylus* „ . .	Zittel, Palæontographica, vol 29, p 64.
	Non *P Kochi*	Winkler, Mus Teyler Archives, vol. 3, 1874, p. 377
Pterodactylus Lavateri, v. Meyer		See ORNITHOPTERUS.
PTERODACTYLUS LIASICUS, Quenstedt . .		(Upper Lias, Lower Lias, and Upper Keuper, Würtemberg.)
1858	*Pterodactylus* . .	Quenstedt, 'Der Jura,' p. vi.
1858	„ *Liasicus* . .	Quenstedt, Jahresheft. Naturk. Wurttemb., vol. 14, p. 299.
1860	„ „ . .	v. Meyer, 'Fauna d. Vorwelt, Rept Lithog. Schief.,' p. 66.
Pterodactylus longicaudus, Münster . .		See RHAMPHORHYNCHUS.
PTERODACTYLUS LONGICOLLUM, v. Meyer . .		(Lithographic Slate, Eichstätt, Bavaria.)
1854.	*Pterodactylus longicollum* . .	v. Meyer, Neues Jahrb. Mineral, p. 52.
1858	„ *longicollis* .	Wagner, Munchen, Bayer. Akad Abhandl., vol. 8, pt. 2, p. 456
1860	„ *longicollum* . . .	v. Meyer, 'Fauna d. Vorwelt, Rept. Lithog. Schief.,' p 45.
1861	„ *longicollis* . .	Wagner, München, Bayer Akad. Sitzber., p. 532
1871	*Diopecephalus longicollum* . .	Seeley, Ann. Mag Nat. Hist., ser. 4, vol. 7, p. 35, note.
PTERODACTYLUS LONGIPES, Munster . . .		(Lithographic Slate, Solenhofen, Bavaria.)
1836	*Pterodactylus longipes* . .	Münster, Neues Jahrb Mineral., p. 580.
1860.	„ „	v Meyer, 'Fauna d. Vorwelt. Rept. Lithog. Schief.,' p 48.
1861.	„ „ . .	Wagner, as subspecies of *P longicollis*, Munchen, Bayer. Akad Sitzber., vol 1, p 532.
Pterodactylus longirostris, Cuvier . . .		See PTERODACTYLUS ANTIQUUS
Pterodactylus macronyx, Buckland . .		See DIMORPHODON.
PTERODACTYLUS MANSELI, Owen		(Kimeridge Clay, Dorsetshire)
1874	*Pterodactylus Manseli* . .	Owen, Pal. Soc., Mesoz Rept., pt 1, p. 8, pl. 1.
PTERODACTYLUS MARDERI, Owen . .		(Lias, Lyme Regis)
1874.	*Pterodactylus Marderi* . .	Owen, Pal. Soc., Mesoz. Rept., pt. 1, p 12.
PTERODACTYLUS MEDIUS, Munster . .		(Lithographic Slate, Daiting, Monheim, Bavaria)
1831.	*Pterodactylus medius* . . .	Munster, Nova Acta Leopold., vol. 15, pt. 1, p 49.
1831.	„ *intermedius* . . .	Goldfuss (in error), *ibid*, p 68
1860	„ *medius*	v. Meyer, 'Fauna d. Vorwelt, Rept. Lithog. Schief.,' p. 39.
1861.	„ „	Wagner, as subspecies of *P. propinquus*, München, Bayer. Akad. Sitzber., p. 532.
Pterodactylus Meyeri, Münster		See PTENODRACON BREVIROSTRIS.
Pterodactylus micronyx, Meyer		See PTERODACTYLUS REDENBACHERI.
Pterodactylus Montanus, Marsh		See DERMODACTYLUS.
Pterodactylus Münsteri, Goldfuss		See RHAMPHORHYNCHUS.

Pterodactylus nettecephaloides, Ritgen		See PTENODRACON BREVIROSTRIS
Pterodactylus nobilis, Owen		See ORNITHOCHEIRUS
Pterodactylus occidentalis, Marsh		See PTERANODON
PTERODACTYLUS ORNIS, Giebel		(Wealden, Tilgate)
1840	Bones of Birds	Mantell, Geol Soc Trans, ser 2, vol 5, p 175
1846	*Pterodactylus*	v. Meyer, Palæontographica, vol 1, p 2
1846	„	Owen, Geol. Soc Quart. Journ, vol 2, p 96
1847	„ *ornis*	Giebel, 'Fauna d Vorwelt,' vol 1, p 99
1872.	„ „	Sauvage, Soc Géol France Bull, ser 3, vol 1, p 365
Pterodactylus Oweni, Marsh		See PTERANODON OCCIDENTALIS
PTERODACTYLUS PLEYDELLI, Owen		(Kimeridge Clay, Dorsetshire)
1874.	*Pterodactylus Pleydelli*, Owen	Pal. Soc, Mesoz Rept, pt 1, p 9
PTERODACTYLUS PROPINQUUS, Wagner		(Lithographic Slate, Bavaria)
1857.	*P. (Ornithocephalus) propinquus*	Wagner, München, Bayer Akad Anzeig, 17th August, 1857, p 171
1858	*Pterodactylus propinquus*	Wagner, München, Bayer Akad. Abhandl, vol 8, pt 2, p 451
1860	„ „	v Meyer, 'Fauna d Vorwelt, Rept Lithog Schief,' p. 40.
1861.	„ „	Wagner, München, Bayer Akad Sitzber, vol 1, p 532. (Wagner includes *P. medius* as a subspecies.)
Pterodactylus pulchellus, v. Meyer		See PTERODACTYLUS ELEGANS
PTERODACTYLUS REDENBACHERI, Wagner		(Lithographic Slate, Solenhofen, Bavaria)
1851	*Ornithocephalus Redenbacheri*	Wagner, Munchen, Bayer Akad Anzeig, No. 35, p 270.
1856.	*Pterodactylus micronyx*	v. Meyer, Neues Jahrb Mineral, p 826
1858	„ „	Wagner, as subspecies of *P. Kochi*, Munchen, Bayer Akad Abhandl., vol 8, pt 2, p 518
1860.	„ „	v Meyer, 'Fauna d Vorwelt, Rept Lithog. Schief,' p. 59.
1861.	„ „	Wagner, München, Bayer. Akad. Sitzber., vol 1, p 524
1861.	„ *Redenbacheri*	Wagner, *ibid.*, vol. 1, p. 532
1861.	„ *micronyx*	v Meyer, Palæontographica, vol 10, p 47.
1863.	„ „	v. Meyer, Neues Jahrb Mineral., p. 247.
1870.	„ „	Winkler, 'Descript Nouvel Exemplaire,' Harlem
1871.	„ „	Winkler, Neues Jahrb Mineral, p 112.
1874.	„ „	Winkler, Mus. Teyler Archives, vol 3, p 84
PTERODACTYLUS RHAMPHASTINUS, Wagner		(Lithographic Slate, Bavaria)
1851.	*Ornithocephalus rhamphastinus*	Wagner, Munchen, Bayer Akad. Sitzber., vol 6, pt 1, p 132
1860.	*Pterodactylus rhamphastinus*	v. Meyer, 'Fauna d Vorwelt, Rept. Lithog Schief.,' p 54
1861.	„ „	Wagner, Munchen, Bayer Akad Sitzber, p 531
1874.	*Diopecephalus* „	Seeley, Ann Mag. Nat Hist, ser. 4, vol 7, p 35, note
Pterodactylus sagittirostris, Owen		See ORNITHOCHEIRUS.
Pterodactylus scolopaciceps, v. Meyer		See PTERODACTYLUS KOCHI.
PTERODACTYLUS SECUNDARIUS, v. Meyer		(Lithographic Slate, Bavaria.)
1843.	*Pterodactylus secundarius*	v Meyer, Neues Jahrb. Mineral, p. 583.
1851.	*Ornithocephalus* „	Wagner, München, Bayer. Akad. Abhandl, vol. 6, pt. 1, p. 178, and pt 3, p 690
1860.	*Pterodactylus* „	Frischmann, Neues Jahrb Mineral., p. 31.
1861.	„ „	Wagner, as subspecies of *P. longicollis*, München, Bayer Akad. Sitzber., p. 532.
Pterodactylus Sedgwickii, Owen		See ORNITHOCHEIRUS.

Pterodactylus simus, Owen . .	See ORNITHOCHEIRUS.
PTERODACTYLUS SPECTABILIS, v. Meyer	(Lithographic Slate, Bavaria.)
1861 *Pterodactylus spectabilis* . .	v. Meyer, Neues Jahrb. Mineral., p 467
1861. ,, ,, .	v. Meyer, Palæontographica, vol. 10, p. 1.
1863 ,, ,,	v. Meyer, Neues Jahrb. Mineral., p. 247.
1882 ,, ,, .	Zittel, Palæontographica, vol. 29, p 77.
Pterodactylus Suevicus, Quenstedt .	See CYCNORHAMPHUS.
PTERODACTYLUS SUPRAJURENSIS, Sauvage .	(Kimeridgian, Boulogne.)
1873. *Pterodactylus Suprajurensis* . .	Sauvage, Soc Géol France Bull., ser. 3, vol. 1, p 365
Pterodactylus umbrosus, Cope . . .	See PTERANODON INGENS.
Pterodactylus validus, Owen . .	See ORNITHOCHEIRUS
Pterodactylus velox, Marsh	See PTERANODON.
PTERODACTYLUS VULTURINUS, Wagner . .	(Lithographic Slate, Daiting, Monheim, Bavaria.)
1857. *P. (Ornithocephalus) vulturinus*	Wagner, Munchen, Bayer. Akad. Anzeig., No. 21, p 174.
1860 *Pterodactylus* ,,	v. Meyer, 'Fauna d Vorwelt, Rept. Lithog Schief.,' p. 62.
1861 ,, ,,	Wagner, München, Bayer. Akad. Sitzber., vol. 1, p. 531.
Pterodactylus Woodwardi, Owen	See ORNITHOCHEIRUS.
Pterodactylus Württembergicus, Quenstedt	See CYCNORHAMPHUS SUEVICUS.
Pycnorhamphus, Zittel	In error for PACHYRHAMPHUS. (See Palæontographica, vol. 29, 1882, p. 80.)
RHAMPHOCEPHALUS BUCKLANDI, v. Meyer . .	(Stonesfield Slate.)
1832. *Pterodactylus Bucklandi* . . .	v. Meyer, 'Palæologica,' pp. 117 and 252.
1859. ,, ,, . . .	Huxley, Geol. Soc. Quart. Journ., vol. 15, p. 658.
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1874 ? ,, *Duncani*. . .	Owen, Pal. Soc., Mesoz Rept., pt. 1, p. 11, pl. 1, fig. 18.
1874. ? ,, *Kiddi* . . .	Owen, *ibid.*, pl. 1, fig. 17.
1888. *Rhamphocephalus Bucklandi*	Lydekker, 'Cat. Foss Rept. Brit. Mus.,' p. 34.
RHAMPHOCEPHALUS DEPRESSIROSTRIS, Huxley	(Stonesfield Slate.)
1859. *Rhamphorhynchus depressirostris*	Huxley, Geol. Soc. Quart. Journ., vol. 15, p. 663.
1874. ? *Pterodactylus Aclandi* .	Owen, Pal. Soc. Mesoz Rept., pt 1, p. 11.
1888. *Rhamphocephalus depressirostris*	Lydekker, 'Cat. Foss. Rept. Brit Mus.,' p. 11.
RHAMPHOCEPHALUS PRESTWICHI, Seeley .	(Stonesfield Slate, Kineton, Warwick.)
1880. *Rhamphocephalus Prestwichi* .	Seeley, Geol. Soc. Quart. Journ., vol. 36, p. 27.
1885 *Dolichorhamphus* (in error) . .	Seeley, Phillips' Geology, edit. 2, p. 518.
Rhamphorhynchus Banthensis, Theodori .	See DORYGNATHUS.
Rhamphorhynchus Bucklandi, v Meyer . .	See RHAMPHOCEPHALUS
Rhamphorhynchus crassirostris, Goldfuss . .	See SCAPHOGNATHUS.
Rhamphorhynchus curtimanus, Wagner	See RHAMPHORHYNCHUS MÜNSTERI.
Rhamphorhynchus depressirostris, Huxley	See RHAMPHOCEPHALUS.
Rhamphorhynchus ensirostris, Theodori . .	See DORYGNATHUS BANTHENSIS.
RHAMPHORHYNCHUS GEMMINGI, v. Meyer .	(Lithographic Slate, Solenhofen, Bavaria.)
1846. *P.* (*Rhamphorhynchus*) *Gemmingi*	v. Meyer, Palæontographica, vol. 1, p. 1, and Neues Jahrb. Mineral., p. 463.
1851. *Ornithocephalus* .	Wagner, München, Bayer. Akad. Abhandl., vol. 6, pt. 1, p. 190.
1855. *Rhamphorhynchus*	v. Meyer, Neues Jahrb. Mineral., pp. 333 and 809.
1858. *longimanus* . .	Wagner, München, Bayer Akad Abhandl., vol 8, pt. 2, p. 491.

1860	*Rhamphorhynchus Gemmingi*	v Meyer (in part), 'Fauna d. Vorwelt, Rept Lithog. Schief.,' p 67
1870	„ *Meyeri*	Owen, Pal Soc., Lias Rept, pt 2, p 80, pl 19, fig. 5
1882	„ *Gemmingi*	Zittel, Palæontographica, vol 29, p. 51.
	Rhamphorhynchus Goldfussi, Theodori	See DORYGNATHUS BANTHENSIS
	RHAMPHORHYNCHUS GRANDIS, Cuvier	(Lithographic Slate, Solenhofen, Bavaria.)
1824	*Pterodactylus grandis*	Cuvier, 'Oss Foss.,' edit 3, vol 5, pt 2, p 380.
1851.	*Ornithocephalus* „	Wagner, Munchen, Bayer. Akad. Abhandl., vol. 6, pt 1, p 190
1860.	*Pterodactylus* „	v. Meyer, 'Fauna d Vorwelt, Rept Lithog Schief.,' p 61
1861	„ „	Wagner, Munchen, Bayer Akad Sitzber., vol 1, p 531.
	RHAMPHORHYNCHUS LONGICAUDA, Münster	(Lithographic State, Eichstatt, Bavaria)
1839	*Pterodactylus longicaudus*	Munster, Neues Jahrb Mineral., p 677
1851	*Ornithocephalus* „	Wagner, Munchen, Bayer Akad. Abhandl., vol 6, pt 1, p 168
1860	*Rhamphorhynchus* „	v. Meyer, 'Fauna d. Vorwelt, Rept Lithog Schief.,' p. 81
1861	„ „	Wagner, Munchen, Bayer. Akad Abhandl., vol. 9, p 113
1861	„ „	Wagner, Munchen, Bayer Akad Sitzber., vol 1, p 535
1882	„ „	Zittel, Palæontographica, vol. 29, p 54
1884	„ „	Ammon, Regensburg, Nat Ver Corr Blatt, vol. 38, p 130.
	Rhamphorhynchus longimanus, Wagner	See RHAMPHORHYNCHUS GEMMINGI
	Rhamphorhynchus macronyx, Buckland	See DIMORPHODON.
	Rhamphorhynchus Meyeri, Owen	See RHAMPHORHYNCHUS GEMMINGI
	RHAMPHORHYNCHUS MÜNSTERI, Goldfuss	(Lithographic Slate.)
1831	*Ornithocephalus Munsteri*	Goldfuss, Nova Acta Leopold., vol. 15, pt. 1, p 112.
1832.	*Pterodactylus* „	v Meyer, 'Palæologica,' pp. 116 and 248.
1846.	*P (Rhamphorhynchus) Munsteri*	v Meyer, Palæontographica, vol 1, p 20.
1851.	*Ornithocephalus Munsteri*	Wagner, Munchen, Bayer. Akad Abhandl., vol 6, pt 1, p 172
1857.	*P (Rhamphorhynchus) hirundinaceus*	Wagner, Munchen, Bayer. Akad. Anzeig., No 22, p 180
1858.	*Pterodactylus Munsteri*	v. Meyer, Neues Jahrb Mineral., p 62
1858	„ „	Wagner, Munchen, Bayer Akad. Abhandl., vol 8, pt. 2, p. 521
1858	*Rhamphorhynchus curtimanus*	Wagner, *ibid.*, pp. 481, 483, 491.
1858.	„ *hirundinaceus*	Wagner, *ibid.*, pp 485, 522
1860	„ *Gemmingi*	v. Meyer (in part), 'Fauna d Vorwelt, Rept Lith Schief.,' p 67
1860.	„ „	v. Meyer, Palæontographica, vol. 7, p 79
1882	„ *phyllurus*	Marsh, Amer Journ Sci., ser. 3, vol 23, p 256.
1882	„ *Munsteri*	Zittel, Palæontographica, vol 29, p 49.
	Rhamphorhynchus phyllurus, Marsh	See RHAMPHORHYNCHUS MÜNSTERI
	SCAPHOGNATHUS CRASSIROSTRIS, Goldfuss	(Lithographic Slate, Bavaria).
1831	*Pterodactylus crassirostris*	Goldfuss, Nova Acta Leopold., vol 15, pt. 1, p 63.
1836	„ „	Buckland, Bridgewater Treatise, p 221
1843	*Pachyrhamphus* „	Fitzinger, 'Systema Reptilium,' p 35
1851.	*Pterodactylus* „	Owen, Pal Soc., Cret Rept, pl. 27, figs 2, 3, 4.
1851	*Ornithocephalus* „	Wagner, Munchen, Bayer Akad Abhandl., vol 6, pt. 1, p. 189
1852	*Brachytrachelus* „	Giebel, 'Allgemeine Palæont.,' p. 231
1858	*Rhamphorhynchus* „	Wagner, München, Bayer Akad Abhandl., vol. 8, pt. 2, p. 505.
1860	*Pterodactylus* „	v. Meyer, 'Fauna d. Vorwelt, Rept Lithog Schief.,' p 40
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1882.	*Pachyrhamphus* „	Zittel, Palæontographica, vol. 29, p 17.
1888.	*Scaphognathus Purdoni*, Newton	(Upper Lias, Yorkshire).

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XX. *The Electric Organ of the Skate.—The Electric Organ of* Raia radiata.

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[PLATES 79, 80.]

The Structure of the Electric Organ of Raia radiata.—The development of the electric discs of *Raia batis* and the structure of the electric cups of *Raia circularis* having been already described,[*] I shall now give an account of the organ of *Raia radiata*, partly by way of indicating in what respects it differs in structure from the organ of the species *batis* and *circularis*, and partly by way of describing the development of electric cups.

In considering the organ of *Raia radiata* it is necessary to bear in mind that the species *radiata* differs greatly in size from both *batis* and *circularis*. While *Raia batis* sometimes reaches a length of 6 feet (180 cm), and *Raia circularis* may be over 3 feet (90 cm.), *Raia radiata* seldom exceeds 18 inches (45 cm.) from tip to tip.

The largest of many specimens of *R. radiata* sent to the laboratory was only 19 inches (48 cm.) in length In this specimen the tail, which was thick and broad at the base, measured 9½ inches in length (24 cm), and the electric organ was in the form of a narrow band (Plate 79, fig 1) pointed at both ends, which measured only 13 cm (5⅛ inches) in length and 2 mm. in thickness at the central portion, where the circumference was 9 mm.

In a large *R. batis* the electric organ may be 2 feet (61 cm) in length, and nearly 3 inches (7 cm) in circumference at the centre. There is thus a marked difference in both the absolute and relative size of the organ. This difference, however, seems to depend on the difference in the development of the tail in the two species. In *R. batis*, when the organ first appears the tail (Plate 66, fig. 1) is relatively long, and the caudal muscles form a considerable mass at each side of the vertebral column. In *R. radiata*, on the other hand, the adult form is reached before the conversion of the muscular fibres into electric elements sets in. Plate 79, fig. 3, represents (natural size) a young *R radiata*, in which certain muscular fibres (*o.*, fig 2A) in the region of the tail were in process of developing into electric clubs. In this sketch it will be observed that the tail, though thick at the base, rapidly tapers towards the extremity In transverse sections it was ascertained that this tapering was chiefly due to a reduction of the lateral muscles, more especially of the portion (*m m*, fig 2A) at each side of the tail, from which the electric organ of the Skate is derived Owing apparently to this reduction of the tail of the young *R radiata*, the electric organ, when it eventually appears, differs greatly from that of *R batis*, both in size and position. While in the species *batis* the posterior three-fourths of the organ extends from the skin covering the outer aspect of the tail to the vertebral centra, in *radiata* it occupies a long narrow space or cleft running parallel to the lateral line, and is completely separated from the vertebral column by a relatively thick layer of muscles —the superior and inferior divisions of the caudal muscles. The form and position of the organ are indicated in figs. 1 and 2B, Plate 79 Fig. 2B, shows the organ (*o.*) in contact with the skin, the nerve (*n*) of the lateral line, and portions of the muscles (*m*), which lie between the organ and the vertebral column.

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[*] 'Phil. Trans ,' B, 1888, pp 399–416, Plates 66–68

But not only is the organ of the species *radiata* relatively extremely small; the elements of which it consists are likewise small and far less highly elaborated structures than either the discs of *R. batis* or the cups of *R. circularis.* The difference in size between the cups of large specimens of *R. radiata* and *R. circularis* will be readily ascertained by comparing Plate 80, fig. 12, with Plate 68, fig. 2, which represent the respective cups drawn with the same lenses (ZEISS AA, and ocular No. 12) and camera.

But the difference in the external size of the cups in the two species does not represent the principal difference. Two cups having the same external size may, owing to the difference in the thickness of their walls, differ greatly in their capacity. In *R. circularis* (Plate 68, figs 2 and 4) each electric cup is well moulded, has a deep cavity and thin uniform walls; while in *R. radiata* (Plate 80, fig 12) the cups, as already mentioned, are not only smaller than in *R. circularis*, but, owing to the great thickness of their walls, they are also very much shallower.

By studying sections and teased preparations, it is at once evident that, while the cups of *R. radiata* generally resemble those of *R. circularis*, they differ from each other considerably in detail, more especially in the structure of the walls of the cups and the thickness of the cortex.

The electric layer in *R radiata*, owing to the shallowness of the cups, is necessarily limited in extent; and, although it seems to extend slightly over the rim of the cup, it probably presents only about one-eighth of the surface provided for the terminal nerve fibres by the electric layer in the cups of *R. circularis.* Further, although the electric layer contains distinct oval and round nuclei, it is extremely thin, and does not seem to consist of two distinct laminæ, as is the case in both *R. batis* and *R. circularis.* In connection with the electric layer of each cup there is an extremely rich bunch of nerve fibres (fig. 10). The nerves which supply the respective cups, as indicated in Plate 80, fig. 10, begin to branch a considerable distance in front of the electric plate, and by dividing again and again they give rise to a complex nerve cone, the terminal branches of which appear to form a continuous network immediately in front of the electric layer

It will be instructive to compare the nerve cone of *R radiata* (Plate 80, fig 10) with the nerve layer in *R. batis* (Plate 67, fig. 13) and *R circularis* (Plate 68, fig 4) It is easy to understand how the cone of *R radiata* might assume the form which obtains in *R circularis*, and how by an expansion of the electric plate the arrangement in *R. circularis* would pass into that of *R. batis.* In fresh sections, and in sections fixed with osmic acid, the nerves and the numerous nuclei on their sheaths are readily made out As in the other species referred to, the smaller branches retain only the grey sheath, and the spaces between the nerve fibres are occupied by gelatinous tissue. In *R. radiata* capillaries wind in and out amongst the nerves in front of the electric plate, while in the species *batis* and *circularis* capillaries seem to be entirely absent from the nerve layer. Immediately behind the electric plate in the species *batis* and *circularis* there lies the striated layer, made up of characteristic sinuous lamellæ In *circularis* this layer supports the electric plate and forms the chief portion of the walls of the well moulded cup. In *R. radiata*, on the other hand, the striated layer can scarcely be said to exist. In its place, as represented in Plate 80, fig. 12, supporting the electric plate and forming the great bulk of the shallow thick-walled cup, is a mass of apparently only slightly altered muscular tissue, with nuclei scattered through its substance The difference between the walls of the cups of *R. radiata* and those of *R. circularis* and the striated layer of *R. batis* will be best understood by comparing Plate 80, fig. 12, with Plate 68, fig 5 and Plate 67, fig 13. As shown in Plate 80, fig 12, the entire thickness of the walls of the fully developed cup of *R. radiata* is composed of distinctly striated tissue (containing numerous nuclei), which more closely resembles ordinary muscular fibres than does the head of the clubs (Plate 66, fig 3) of *R. batis.* This resemblance to a muscular fibre is equally well marked in the centre and at the periphery of the cup in question.

In *R circularis* the striation of the striated layer differs decidedly from the transverse striation of a muscular fibre. Instead of presenting simple parallel lines, as in ordinary muscular fibres, the striated layer (Plate 68, fig. 5) presents a series of extremely sinuous lines, which makes it difficult, at first sight, to believe that the striated layer consists of altered muscular tissue. In *R batis* the striated layer very closely resembles that of *R. circularis;* the contortions are often quite as well marked, but apparently it has departed further from ordinary muscular tissue, in as far as the muscle nuclei have entirely disappeared. Whether the striated layer retains any of the contractile properties of muscular tissue in any of the three species of Skate referred to has not yet been determined; but, from the appearance presented by the cups of *R. radiata*, one might almost expect that it would respond (though, perhaps, very feebly) to stimulation like an ordinary muscular fibre.

Extending backwards from the cup of *R. radiata* is a long tapering stem, sometimes flattened, sometimes bayonet-shaped, but seldom rounded or symmetrical in the fully formed cups. The shape seems to depend chiefly on the amount of compression the adjacent cups produce on one another. In many cases the base of the stem forms an irregular triangle, while the terminal portion is oval or ribbon-shaped. In all cases the stem consists of more or less altered muscular tissue. Sometimes the striations are distinct throughout the whole length; at other times they are obscure in at least the middle portion, while the terminal portion may be crowded with nuclei—thus suggesting degenerative changes. Surrounding the cup and its stem there is a thin nucleated membrane, which, while it seems to represent the thick cortex of *R. circularis* and the alveolar layer of *R. batis*, differs but little from the sarcolemma of an ordinary muscular fibre

The cups are invested by connective tissue, which further fills up the spaces between them, and forms for them a delicate framework. This connective tissue consists partly of fine fibres and partly of gelatinous material. In addition to binding the cups together, so as to form the long narrow electric spindle, the connective tissue serves as a highway for the nerves passing to the cups, and for the blood vessels from which they derive their nourishment. Scattered through the connective tissue are a number of nuclei.

The Development of the Electric Organ of Raia radiata.—As in *Raia batis*, the electric elements are developed out of muscular fibres. In the species *batis*, as already pointed out some of the muscular fibres at each side of the caudal portion of the notochord have assumed the form of clubs when the embryo is 7 cm. in length, and before it escapes from the purse the electric discs are often well advanced towards completion. In *R. radiata*, although the rate of the development of the embryo seems to be slower than in *R. batis*, I have been unable to detect any change in the muscular fibres until the development of the Skate was completed. The youngest specimen of *R. radiata* in which a rudiment of the electric organ could be detected is represented (nat. size) in Plate 79, fig. 3. This Skate measured nearly 9 cm. across the pectoral fins, and was over 12 cm. in length. Hence, it may be presumed that it was three or four times the age of the embryo *R. batis* (Plate 66, fig. 1) from which the electric clubs represented in Plate 66, fig. 2 were drawn, and that the electric organ is very much later in appearing in the species *radiata* than in the species *batis*.

As already pointed out, the reduction of the tail (and more especially of the middle section of the caudal muscles on each side) has proceeded further in *R radiata* than in *R batis* before the organ appears. For this reason, the space available (Plate 79, fig. 2A) for the electric organ to develop in is far more limited than in *R batis*.* Probably, for this reason also, only a limited number of muscular fibres are altered in *R. radiata* (about one third of the number in *R. batis*); and it may be for the same reason that instead of forming large discs they give rise to small cups.

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* The amount of raw material out of which the organ is developed is also limited; but this is probably of secondary importance.

The first evident step in the conversion of the muscular fibres destined to form electric elements consists, as in *R. batis*, in the expansion of their anterior ends so that each assumes the appearance of a club (Plate 79, fig 3A) This process seems to occupy a considerable time, and it takes place without causing any marked change either in the position or structure of the fibres concerned Further, all the fibres are not enlarged simultaneously; while some of the fibres have expanded into distinct clubs, others differ from the adjacent muscles only in having their anterior ends slightly rounded and retracted from the intermuscular septum As the comparative lateness of the conversion of the muscular fibres would lead one to expect, the clubs of *R radiata* are at the outset nearly double the length of the clubs of *R. batis* In other words, the muscular fibres in *R radiata* are nearly double the length of the fibres in *R batis* when the process of conversion first sets in. This difference in the size of the newly formed clubs in the two species will be made evident on comparing Plate 66, fig 2, with Plate 79, figs 4 and 5. In fig 2 the clubs of *R. batis* are represented, while figs 4 and 5 represent on the same scale the clubs of *R radiata* The form of the clubs of *R. radiata* is represented in Plate 79, fig. 3A, in which *a* represents a fibre with the anterior end only slightly expanded, and *b* a fibre which is distinctly club-shaped. As already stated, the clubs are only in process of formation when the young *R. radiata* has reached a length of 12 cm., and measures 9 cm. across the pectoral fins. In *R batis* the clubs appear long before the embryo is hatched, while there is still a large yolk sac, and when the measurement across the pectoral fins is only 2·5 cm. Further, not only does the conversion of the muscular fibres set in sooner in *R. batis* than in *R. radiata,* but the development proceeds so rapidly that before *R. batis* reaches a length of 12 cm. (the length at which the clubs first appear in *R. radiata*) the electric elements are in some respects more fully developed than they are in the adult *R. radiata.*

But the clubs of the two species differ in more respects than in size and time of appearance The clubs in *R. radiata* are not only longer and thicker, they are, in addition, more distinctly striated, and there is no indication of a forward migration of nuclei towards the anterior end, as is the case in the clubs of *R. batis.* From Plate 79, figs. 4 and 5, it will be observed that, although in *R radiata* there is no marked crowding of nuclei in front of and around the head of the club, as is the case in *R. batis,* the nerves are extremely abundant, apparently as numerous as they are at the corresponding stages in *R batis.*

After the clubs have appeared in *R radiata,* they slowly expand and increase in length to form what may be termed secondary clubs (Plates 79 and 80, figs. 6, 7, and 8). These secondary clubs vary considerably in form, and especially in length. Some of them are quite double the length of the primary clubs represented in figs. 4 and 5, but, while the anterior portion has greatly increased in dimensions, the posterior is often reduced to a long slender, though still distinctly striated, process. The difference between the primary and secondary clubs will be seen by referring to Plate 79, fig 7, where two of the primary clubs (*b.*) are represented alongside a number of secondary clubs (*o*). By the time the secondary clubs are formed the young Skate has reached a length of about 18 cm, and the unaltered muscular fibres adjacent to the developing clubs have greatly increased in length, being at least double the length of the longest clubs. In a *R. batis* of about the same length (though, probably, somewhat younger) the electric organ is already made up of complex discs (Plate 67, fig 8) which only essentially differ from the discs of the adult Skate in being of a smaller size. There is thus a striking difference in the club stage of the two species. In *R. batis*, the clubs rapidly enlarge to form shallow cup-shaped bodies, which are as rapidly transformed, first into mushroom-like structures, and then into discs—the cup-stage being reached when the *R. batis* embryo is only some 10 cm. in length, while in *R. radiata*, as already mentioned, a length of 18 cm is reached before the secondary clubs are completed. In all probability the indistinct cup found in embryo specimens of *R batis* corresponds to the well marked cups found in the adult *R. radiata* and *circularis*. If this is the case, it may be inferred that, while the process of conversion of a muscular fibre into an electric element is prolonged in *R. radiata*, it is comparatively rapid in *R batis*, the early stages especially being abbreviated—a state of things advantageous in most cases, but especially so, one would suppose, in an electric organ which is presumably, at the most, of little use during its early stages of development.

But, although in *R. radiata* a considerable time is occupied in converting the muscular fibres into what I have designated secondary clubs—although, as it were, every step in the ancestral history seems to be faithfully reproduced, there is never any indication of the development being arrested nor of retrogressive changes setting in, and this holds for the later as well as the earlier stages, for until the simple electric cup of *R. radiata* is completed (and this only takes place when the Skate is reaching maturity) there is no pause in the process, and when once complete the cup increases in size as the tail of the Skate increases in dimensions.

There is thus a remarkable difference in the history of the muscular fibres which are converted into clubs, and the surrounding fibres which, as it were, become obliterated to make room for the developing electric cups. In fig 2A it will be observed that less than a third (*o*) of the fibres (*m.m.*) seen in transverse section are utilised for the production of electric elements Yet, in fig. 2B, the electric organ (*o*) occupies the entire space between the skin and the superior and inferior caudal muscles (*s i*). It is extremely interesting to study sections between the stages represented in fig. 2, and to note that as the central fibres (*o* , fig. 2) gradually increase in size until they occupy the whole available space, the fibres at each side (*m.m.*) as gradually undergo degenerative changes, and ultimately completely disappear.

As the primary club enlarges, the rounded anterior end becomes truncated, and, later, slightly concave; and at the same time the motor plate increases in size and forms a lining or the shallow depression towards which the ever-increasing nerve fibres extend. These nerve fibres occupy the trumpet-shaped space left as the developing club retracts from the septum to which it was originally connected (Plates 79 and 80, figs. 6 and 8). This space seems to be enclosed by a layer of intermuscular connective tissue. What becomes of the sarcolemma which surrounded the anterior end of the muscular fibre has not been determined; but, in all probability, it remains in contact with the truncated end of the fibre, and eventually blends with and assists in forming the electric plate. The secondary clubs having been completed, they begin to condense, to form the characteristic electric cups. It is impossible to state what time is occupied in passing from the club to the cup stage: when the young *R. radiata* is about 24 cm. in length the moulding has distinctly begun (Plate 80, fig. 9), but even when a length of 35 cm. is reached it is still imperfect (Plate 80, fig. 10), and the cup proper (Plate 80, figs. 11 and 12) does not seem to be completed until a length of nearly 40 cm. is reached, *i.e.*, until the Skate has all but reached maturity. It is somewhat remarkable that while the anterior end of the club is expanding, as represented in figs. 6, 9, and 10, the narrow posterior portion is still increasing in length. An idea of the extent of the changes which take place in a developing cup during the time required for a *R. radiata* to grow from 11 cm. to 35 cm. will be gathered by comparing figs. 3A and 10, which are both drawn to the same scale.

In passing from the club to the cup stage the changes are less abrupt in *R. radiata* than in the species *batis* and *circularis*. The muscular substance of the head of the club, without being transformed into extremely complex sinuous lamellæ, as is the case in *R. circularis* and other forms, is simply moulded to give rise to a rounded shallow cup, such as is represented in fig. 12, every part of which is striated like an ordinary muscular fibre.

Further, numerous nuclei lie in the substance of the cup (fig. 12), and in frozen sections spaces appear in the walls similar to those seen in frozen muscular fibres. As the cup proper resembles in structure a muscular fibre, its investing sheath, as already stated, resembles ordinary sarcolemma. In *R. circularis* nuclei aggregate around the outer surface of the cup, and give rise to a thick cortex (Plate 68, fig. 5). These nuclei in *R. circularis* seem to migrate from the substance of the muscle as it undergoes transformation, but in *R. radiata* this aggregation of nuclei around the outside of the cup is extremely limited, while the nuclei of the muscular wall of the cup retain their original position. This non-migration of the nuclei may to some extent account, on the one hand, for the cup resembling the last muscular tissue, and, on the other, for the absence of a thick cortical layer. The cups when once formed slowly increase in size as the Skate grows larger, and retain their rounded form, except when subjected to pressure by coming into close contact with each other. As the result of pressure, they may assume an oval or somewhat hexagonal form, and the margins may become irregular or even slightly everted.

As the cup stage is reached the stem becomes more distinctly marked off from the cup proper, and loses its rounded contour. Later, it gets compressed, more especially at the base, and in macerated specimens its base sometimes looks extremely broad and transparent from one point of view, but narrow and opaque from another. As the result of compression, the stem often assumes the form represented in figs. 11 and 12; but, even although the terminal portion may be reduced to a narrow thin band with aggregations of nuclei at one or more points, it is never reduced to a short rudiment, as is the case in *R. fullonica* and, to a limited extent, in *R. circularis*, nor does it ever, as far as I have seen, entirely lose its transverse striations.

The electric plate seems to arise in *R. radiata* in very much the same way as in *R. batis*. As in *R. batis*, there is an aggregation of nuclei in front of each club. As the club expands, the nuclei, together with the protoplasm around them, give rise to a thin lining for the shallow muscular cup

At the same time nerves increase in number and in length, and form a rich conical bunch of fibres, which terminate by extremely delicate branches (fig. 12) in the electric plate. While the above changes are taking place the intermuscular connective tissue increases, so as to form a thin gelatinous investment for each cup. It also seems to bind the cups together into a number of short, obliquely directed columns. When these columns are further invested by a delicate sheath the long, slender electric spindle is completed.

Without further exhaustive inquiries, it will be impossible to offer any opinion as to whether the electric organ of the Skate is or is not functionless, or to discuss the uses which the organ has served in the past, or, supposing it to be still functional, to consider how it is of service to the Skate at the present day. But, although a discussion of this nature would, in the absence of sufficient data, be somewhat premature, it may facilitate future inquiries if, by way of concluding this paper, I indicate whether the organ in *R. radiata* may be looked upon as a structure in a state of progressive development, or as a structure which, having been arrested in its development, is now undergoing retrogressive changes. At the outset it may be taken for granted that, either in the Skate group or in some of the ancestors of the Skates, certain muscular fibres in the region of the tail were gradually altered to form electric organs. There is no great difficulty in admitting that under certain conditions muscular fibres might be readily transformed into rudimentary electric plates or discs, but it is still difficult to understand how natural selection could, during the initial stages, step in and take advantage of this variation, and gradually build up complex and, in some cases, extremely useful electric organs. Ordinary muscular fibres may be looked upon as incipient electric elements, for, in addition to their power of contracting, they possess the power of discharging feeble electric currents. It is conceivable that under certain circumstances the one function might be developed at the expense of the other—that the power of contraction would gradually fall into abeyance, while the power of discharging electric shocks would be as gradually increased. [illegible] could we discover a motive for this increased output of electricity during the incipient stages—that even the feeblest electric shocks were of some real use from the outset—the whole mystery as to the evolution of electric organs would at once and for ever vanish.

Granted that under certain conditions muscular fibres are converted into electric organs, and that these conditions still exist and are likely to continue, there is no reason why electric organs should not be in process of elaboration at the present day. Mr. DARWIN, in considering electric organs, points out* that "there is no reason to suppose that they have been inherited from a common progenitor," for, he adds, "had this been the case, they would have closely resembled each other in all respects." Hitherto no trace of an electric organ has been discovered in any of the Selachians, not even in the family Spinacidæ, to which the Skates and Rays are supposed by some to be genetically related. Neither is there reason for supposing that electric organs would have been more useful to the extinct than to the recent members of the Skate family. It is thus possible that the electric organs of the Skates have not been inherited from Shark-like ancestors, and that they were neither larger nor more useful in the extinct than they are in the recent species. There being thus a possibility that the electric organ has reached its maximum size in some Skates during recent times, and that in others it is still in a state of progressive development, or at the most only recently arrested in its development, it is desirable to carefully consider the organ of *R. radiata* with a view to determining, if possible, whether it is a progressing or retrograding structure.

When I first discovered that in some Skates the electric organ consisted of cup-shaped bodies, I was inclined to look upon the cups as primitive structures, which, having been arrested in their growth, had failed to develop into discs, such as exist in *R. batis* and *R. clavata.* I was all the more in favour of this view when I made out that the discs of *R. batis* passed through an indistinct cup stage, and that in *R. radiata* not only were the cups small and simple compared with the discs of *R. batis*, but the entire organ was only a few inches in length, and only about 8 mm. in circumference at its thickest central portion. When, however, I found that the cups in *R. circularis* were large well moulded bodies, with an electric plate nearly as extensive as the electric plate of the disc of *R. batis;* that the electric organ of *R. fullonica*, which also consists of cups, was relatively large and well developed; and that the development of the cups in *R. radiata* was extremely slow; and also that, instead of showing signs of degenerating, they continued to increase in size in the adult forms, it was no longer possible to feel so confident that all the electric organs consisting of cups had been arrested in their development.

Further investigation convinced me that the electric cups were quite distinct structures; that, in fact, while in some Skates the electric elements had assumed the form of discs (*e g.*, *R. batis* and *R. clavata*), in others they had taken the form of cups (*e g.*, *R. circularis* and *R. fullonica*), and that it was as unlikely that a fully developed cup should be converted into a disc as that a disc should be moulded into the form of a cup.*

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* 'Origin of Species,' p 151.

In endeavouring to determine the present *rôle* of the electric organ of *R radiata*, it may be better first to state the arguments in favour of its being a degenerating structure

In favour of degeneration there is first to be mentioned that it has been impossible hitherto to discover any use which the organ of the Skate subserves. If there is a difficulty in discovering the utility of the large electric organ of *R batis*, it may be presumed the difficulty will be still greater in suggesting a use for the smaller organ of *R. radiata.* But the small size of the organ in *R. radiata* may, of itself, be considered an argument in favour of degeneration, or, at least, in favour of its having been arrested in its development; and to the absolute smallness of the organ there is to be added, that the cups composing it are not only extremely minute, but, further, they are remarkably shallow, and hence the electric plate (the most essential part of an electric organ) is very limited in extent. But, as already indicated, the small size of the organ in *R. radiata* has, in all probability, been determined by the size of the tail in this species. It may be supposed that the reduction of the tail in the species *radiata* had proceeded further than in the species *batis* before the electric organ succeeded in establishing itself, and that, in fact, the organ in *R. radiata* is as large as the circumstances attending its development hitherto have rendered possible. It is, of course, impossible to say whether the organ in *R radiata* is now, or in former ages long remained in, or nearly in, a state of arrested development—neither distinctly receding nor advancing.

In a degenerating organ, which appeared at a remote period, we should expect that it would pass rapidly through the early or developmental stages, and that as its possessor continued to increase in size the organ would undergo retrogressive changes, while in an organ that had been simply arrested we should expect that after a certain stage of development had been reached it would remain in a state of comparative quiescence. A reference to the chapter on the development of the organ in *R. radiata* will, however, show that neither of these conditions holds—the development is only completed when maturity is reached, and, once developed, the organ slowly increases in size as the Skate grows larger.

Again, in a degenerating electric organ, we should expect the electric plate to be incomplete, and the nerves passing to it few in number or undergoing retrogressive changes; and one would further expect to find some indication of degeneration of the less essential layers But in *R. radiata* there is a relatively large bunch of well developed nerves proceeding to an electric plate, which is not only complete, but, being apparently in advance of the development of the supporting cup, extends some distance over its margin.

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* But, although the cups and discs are perfectly independent and distinct, there is no reason for supposing that the Skates with cup-shaped organs have sprung from one ancestor, while the Skates with discs have descended from another. The fact that the disc of *R. batis* passes through an indistinct cup stage, points to a common ancestor, in which the electric organ was in all probability made up of slightly altered muscular fibres resembling the clubs of *R. radiata* represented in Plate 79, figs 4 and 5.

In support of the view that the electric organ of *R. radiata* is a progressive structure, or, if not still advancing, that it has been comparatively recently arrested in its progress, there is, first, the remarkable developmental history. I have already pointed out that, while the electric organ of *R. batis* is late in making its first appearance, the organ of *R radiata* is very much later; that, in fact, while in an embryo *R. batis* 12 cm in length the three essential layers of the complex discs have already been established, in a *R. radiata* completely developed and of a considerable size (Plate 79, fig. 3), the muscular fibres (now long and well developed) are only beginning to pass into the primary clubs. I have shown, further, that the clubs pass slowly through a series of intermediate stages before the cup form is assumed, and that the cups when eventually completed slowly increase in size as the Skate increases in length, and that in the largest specimens of *R. radiata* examined there was no indication of degeneration, either in the electric cups or in the nerves passing to them.

In fact, the history of the development of the cups in *R. radiata* seems to be, as far as it goes, a complete record of the more important changes which have taken place in the evolution of electric organs out of muscular fibres. There is at no period any indication of degeneration or any evidence that in *R. radiata* a higher stage of development of the electric organ was ever reached. As one would expect, the electric (motor) plate gradually increases in size, and the muscular fibre is slowly modified to form a suitable support, the fibre retaining, however, its original structure, and, probably, to a certain extent, the power of contracting; and, hence, the transformation is far less complete than in *R. batis*, in which, at the most, only a vestige of the original muscular fibre persists unaltered, the whole of the anterior portion undergoing profound modifications.

Hence, taking into consideration that the young *R. radiata* has reached the adult form before the muscular fibres are converted into clubs, that the clubs are quite double the size of those in *R. batis*, and that, instead of at once giving rise to cups, they form large secondary clubs, and that the cups when they eventually appear in the all but mature Skate retain the characteristic structure of ordinary muscular fibres, and, further, that in the largest specimens examined there was no indication of degeneration in the cups, or of retrogressive changes in the electric plate or its extremely rich supply of nerves, it may, I think, be inferred that in *R. radiata* the electric organ, though relatively extremely small and apparently functionless, is in a state of progressive development.

For material used during this investigation I am chiefly indebted to Messrs. THOMAS SCOTT and PETER JAMIESON, members of the Scientific Staff of the Fishery Board for Scotland, and to Mr. SIM, Naturalist, Aberdeen.

EXPLANATION OF PLATES 79 AND 80

PLATE 79

Fig. 1. Sketch of the electric organ of *Raia radiata*, in a specimen which measured 48 cm. in length. The nerve of the lateral line occupied the groove (*n*) which indents the posterior two-thirds of the outer surface of the organ. Natural size.

Fig. 2. *A*. Transverse section showing the first indication of the electric organ in a young *R radiata* (fig 3) 12 cm. in length.

o. The group of slightly enlarged muscular fibres from which the electric cups are developed.

m The unaltered fibres of the lateral muscular band, most of which, as the organ increases in size, gradually atrophy and disappear.

n. The nerve of the lateral line still separated from the rudimentary organ by a row of muscular fibres.

B. Transverse section of the fully developed electric organ from an adult specimen of *R. radiata* which measured 45 cm. in length.

o. The electric organ lying between the skin and the superior and inferior caudal muscles.

m. Muscular fibres in transverse section.

n. Nerve of the lateral line lying in direct contact with the sheath of the electric organ.

Leitz 00, ocular 3. Outlined with Zeiss' camera.

Fig. 3. Sketch of the smallest *R. radiata* in which muscular fibres were found in process of developing into clubs.

Fig. 3A. Three muscular fibres in process of developing into clubs from the Skate represented in fig. 3. *a*. A fibre with the anterior end only very slightly enlarged. *b*. A fibre which has become distinctly club-shaped and has an enlarged motor plate.

Zeiss AA, compensating eyepiece 12. Outlined with Zeiss' camera.

Fig. 4. A muscular fibre from a *R. radiata* (fig. 3) 12 cm. in length, in which the motor plate and the nerves in connection with it have been considerably enlarged, while the fibre is only very slightly club-shaped.

Zeiss apochromatic 4·00 mm., compensating eyepiece 12. Outlined with Zeiss' camera.

Fig. 5. A muscular fibre which has reached the club stage, from the same Skate as fig. 4. The anterior enlarged end is slightly concave and completely covered

by the motor plate in which the nerve fibres terminate. The striation in this fibre was identical with that of the adjacent muscles.

Zeiss apochromatic 4·00 mm., compensating eyepiece 12. Outlined with Zeiss' camera.

Fig. 6. Two muscular fibres, which resemble Indian clubs, from a Skate (*R. radiata*) measuring 18 cm. These may be known as secondary clubs. The truncated end, which is slightly concave, supports the motor plate, in which numerous nerve fibres terminate. Note that a considerable portion of the muscular fibre takes part in the formation of the club.

Zeiss AA, compensating eyepiece 12. Outlined with Zeiss' camera.

Fig. 7. Sketch of a longitudinal section through part of the tail of a Skate (*R. radiata*) 18 cm. in length, showing from without inwards the skin (*s.*), the nerve of the lateral line (*n.*), the electric organ (*o.*), and portions of muscular fibres (*m.*). Note the oblique arrangement of the secondary clubs, their relative length, and compare them with the two primary clubs (*b.*) from a specimen 12 cm. in length.

Zeiss AA, eyepiece 3. Outlined with Zeiss' camera.

PLATE 80

Fig. 8 shows the secondary clubs, from a specimen 18 cm. in length, more highly magnified than in fig. 7. Observe the difference in the length and diameter of the clubs figured, the nuclei of the motor plate in *A.*, the nerves passing to the motor plate in *B.*, and that the striation of both the head of the club and stem of *B.* resembles the striation of the altered muscular fibre *m.* Had the club *A.* been drawn to the same scale as the clubs represented in figs. 4 and 5, it would have been nearly double the length.

Zeiss DD, ocular 3. Outlined with Zeiss' camera.

Fig. 9. Two muscular fibres in process of changing from clubs into cups from the electric organ of a Skate (*R. radiata*), 24 cm. in length, macerated in nitric acid. Observe that the altered muscular fibres, though nearly double the width of those (fig. 6) from a Skate 18 cm. in length, are only very slightly longer. In some of the developing cups the striation was distinct, and a large bunch of nerves remained in connection with the motor plate.

Zeiss AA, compensating eyepiece 12. Outlined with Zeiss' camera.

Fig. 10. Two fibres which almost reached the cup stage from a Skate 35 cm. in length. The bunch of nerves passing to the motor plate has been represented in *A.*, and their mode of ending in delicate loops and the depth of the cup are indicated in *B.*

Zeiss AA, compensating eyepiece 12. Outlined with Zeiss' camera.

Fig. 11. Sketch showing two cups from the electric organ of a Skate (*R radiata*) which measured 40 cm. in length. Note that the cups, though well moulded, are shallow, and that they lie in close contact with each other Note, also, that the stems have lost their rounded contour, and that, apparently owing to compression, the anterior part of each has been altered so as to present in front a prominent ridge (*r*). By comparing this figure with figs. 6, 9, and 10, an idea will be gained as to the increase in length which has taken place in the stem.

ZEISS AA, compensating eyepiece 12. Outlined with ZEISS'camera.

Fig. 12. Sketch showing two completely developed cups from an adult Skate (*R. radiata*) which measured 45 cm. in length. Compare these with the incompletely formed cups represented in fig. 10, and also with the cup of *R. circularis* (Plate 68, fig. 3) which, though drawn to the same scale, is considerably larger, and has a far more extensive lining (electric plate) and a thick cortex. Observe (1) the thick wall of the shallow cup *A.*, composed of muscular tissue still distinctly striated, with a few muscle nuclei scattered through its substances; (2) the thin electric plate extending over the rim of the cup; (3) the nerves (of which only a few fibres are introduced) which form a continuous series of loops over the electric plate; (4) the thin outer layer (thickened sarcolemma); and (5) the long striated irregularly compressed stem.

ZEISS AA, compensating eyepiece 12. Outlined with camera from cups isolated by maceration

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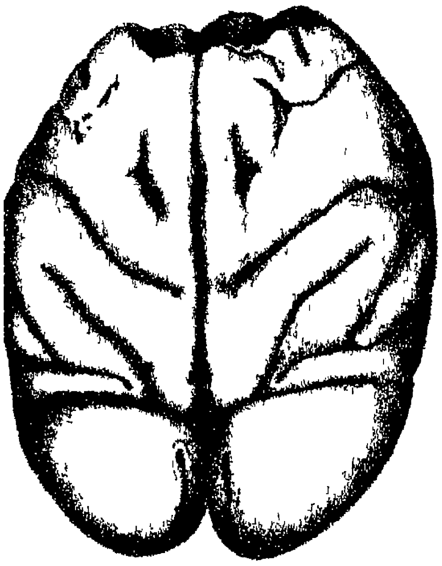

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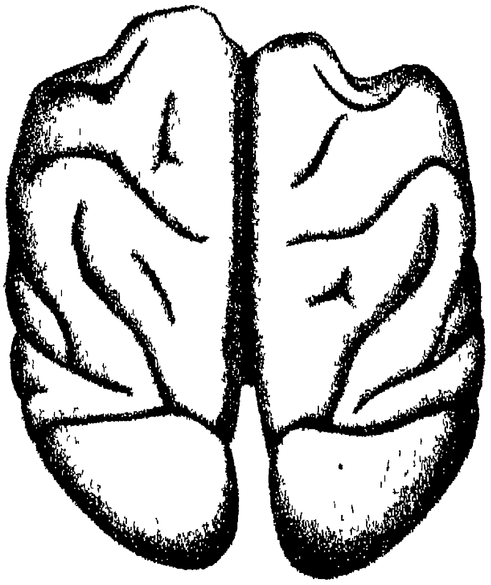

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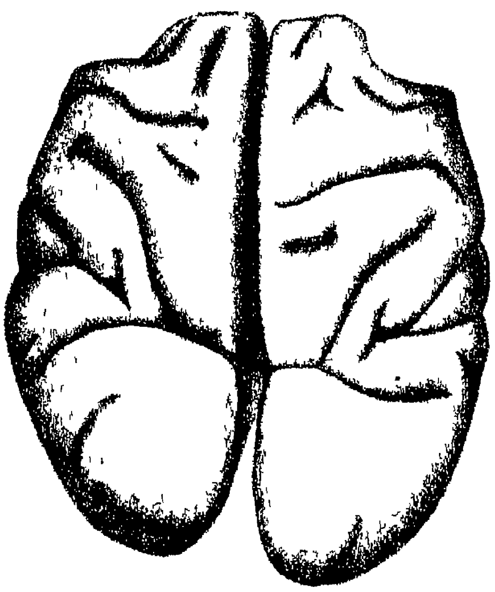

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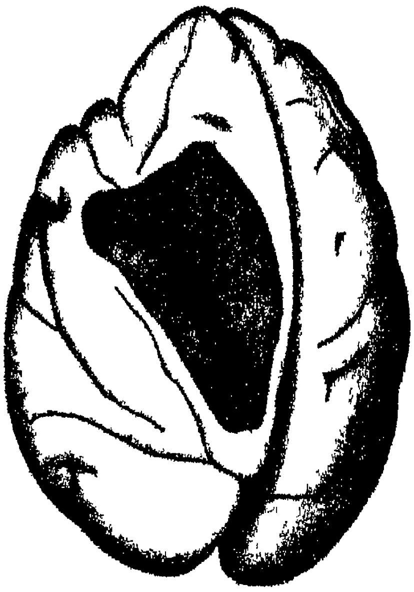

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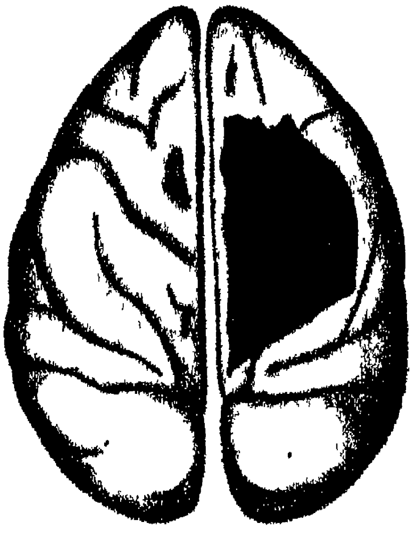

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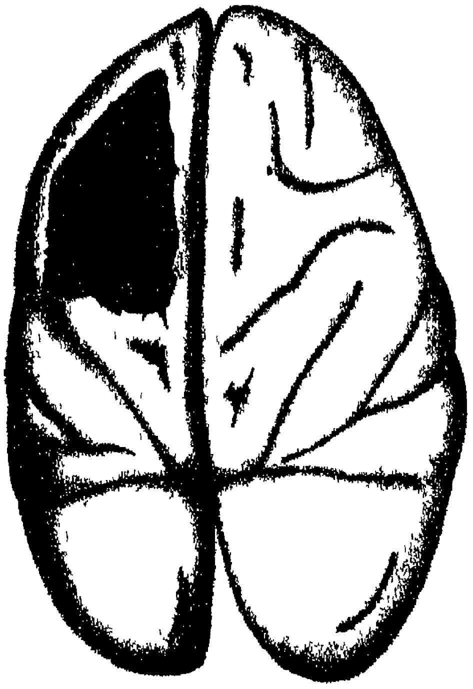

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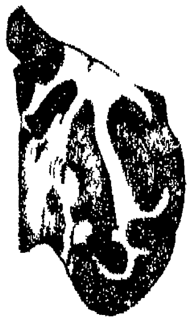

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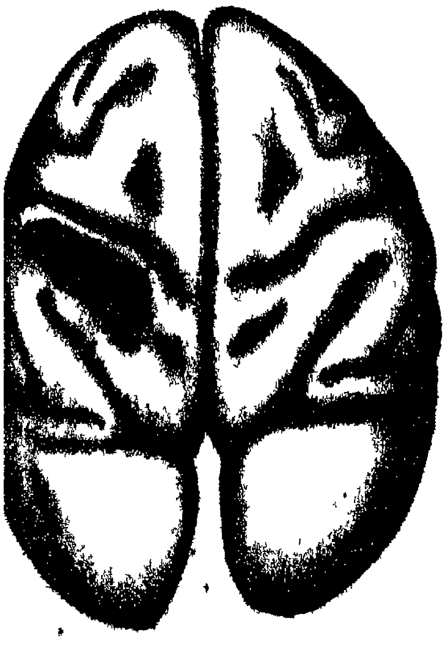

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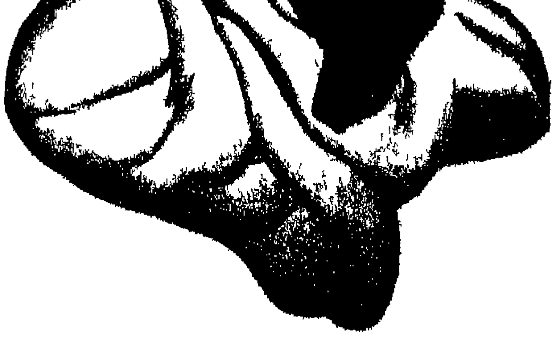

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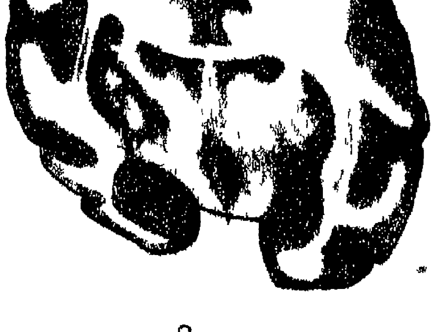

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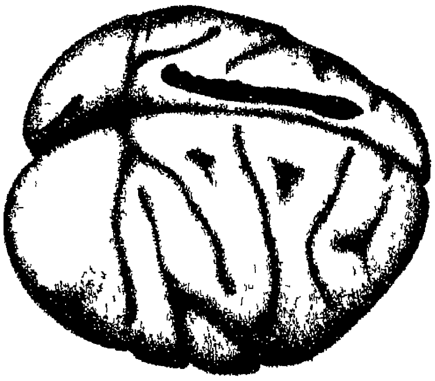
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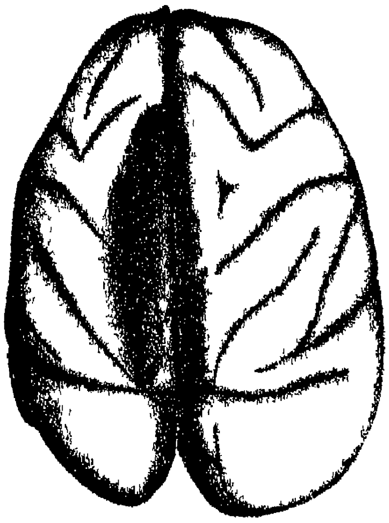
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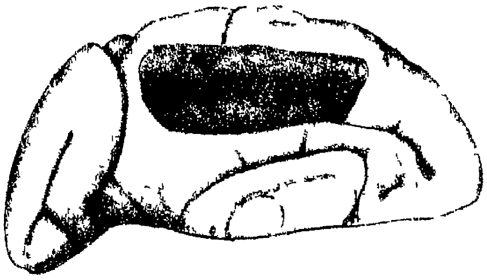
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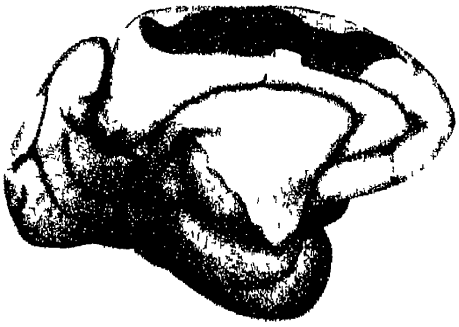
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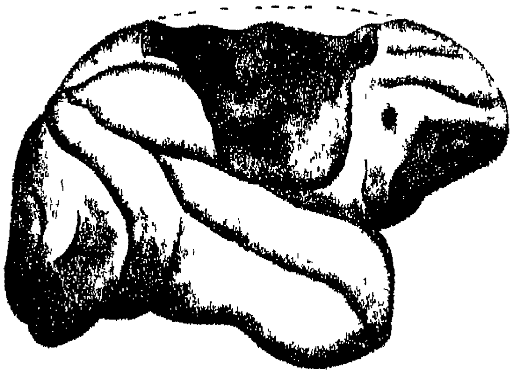
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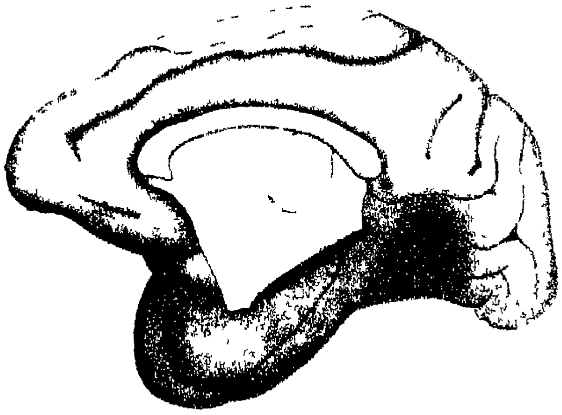
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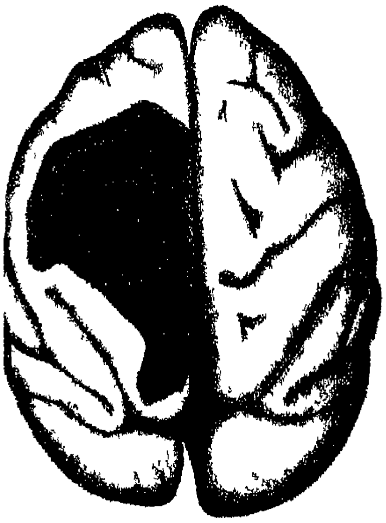
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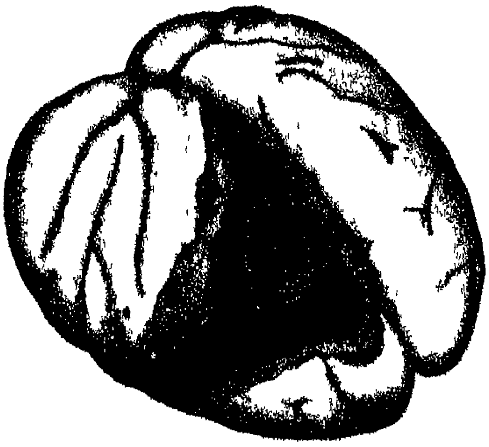
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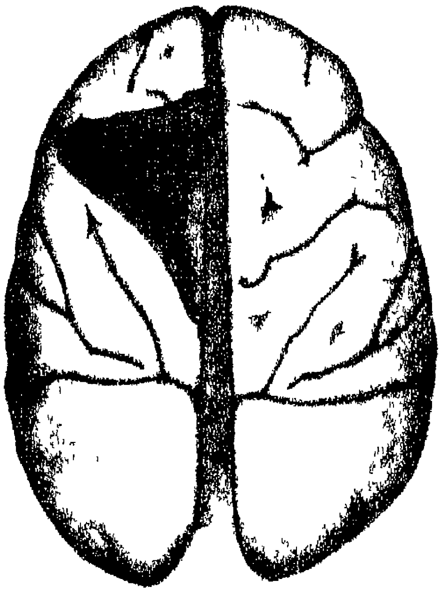
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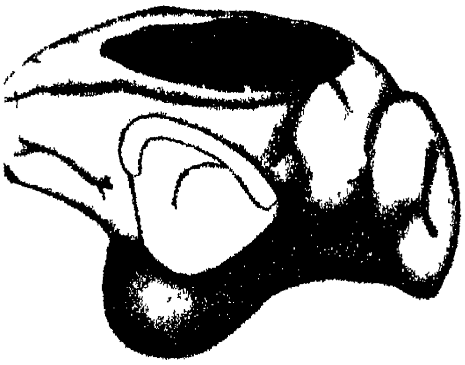
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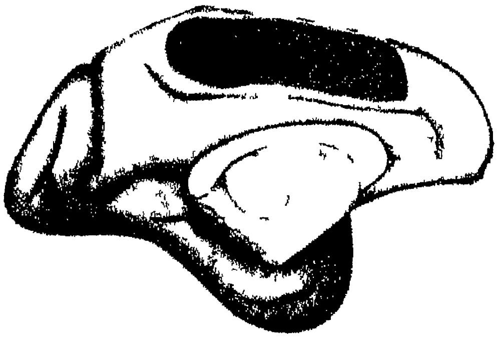
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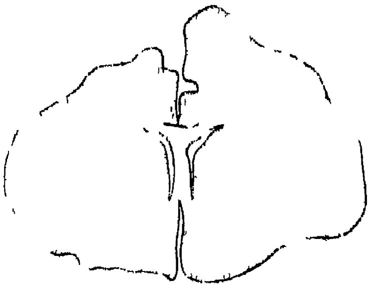
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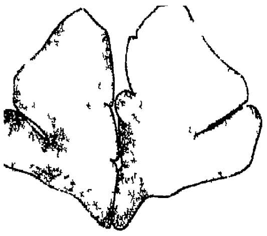

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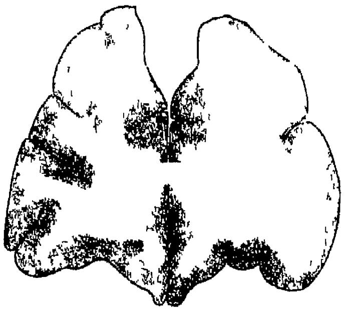

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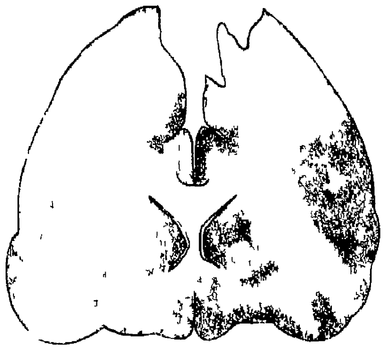

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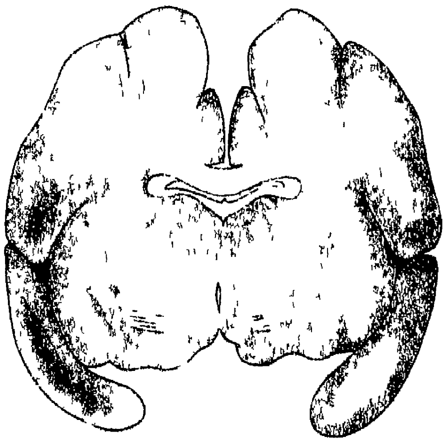

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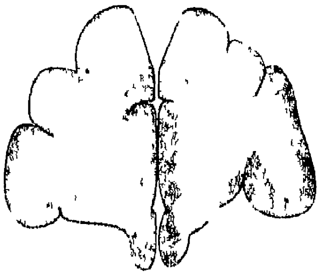

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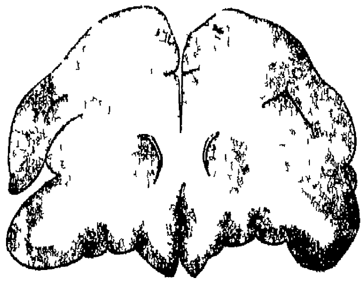

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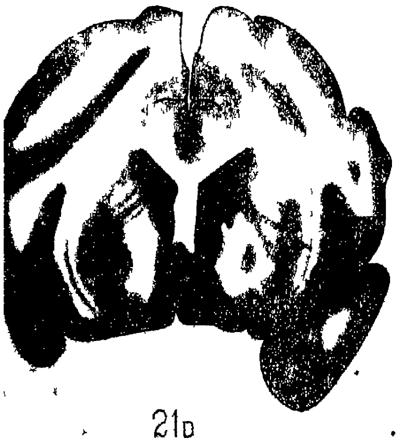

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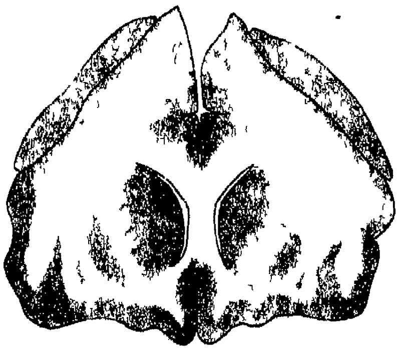

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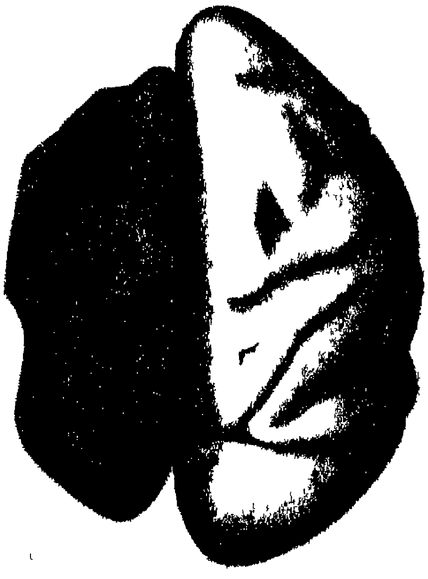

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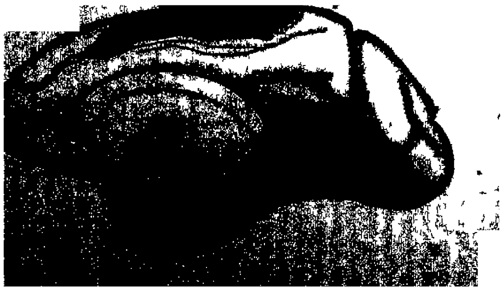

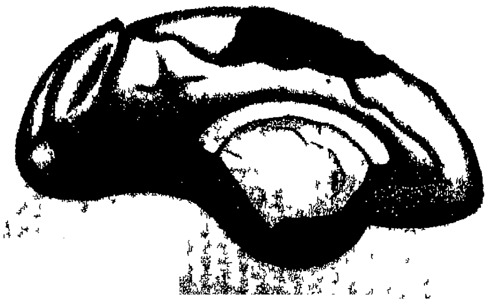

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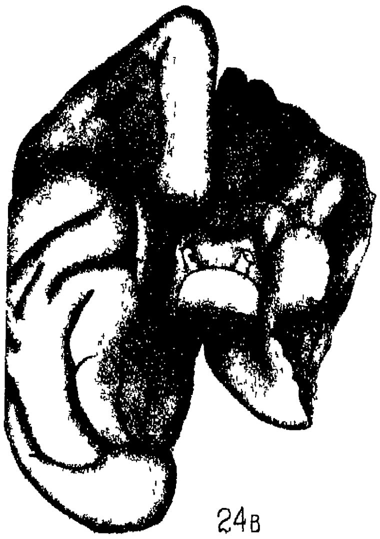
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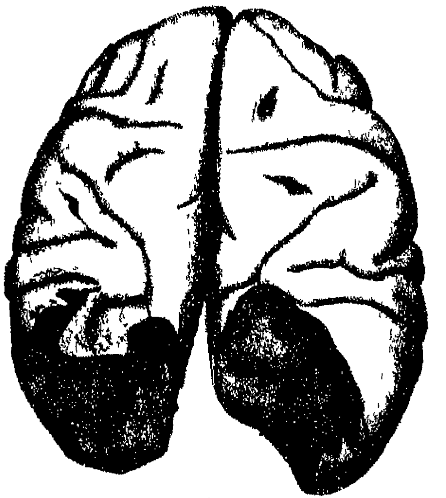
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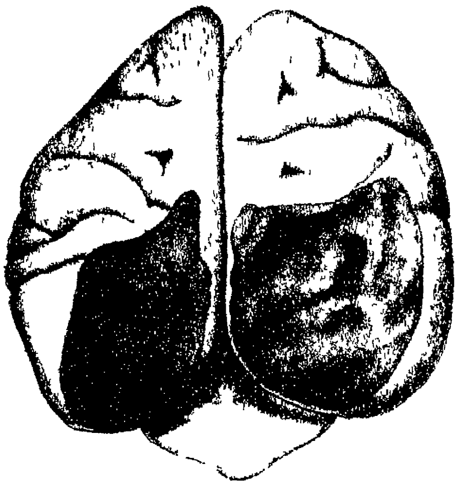
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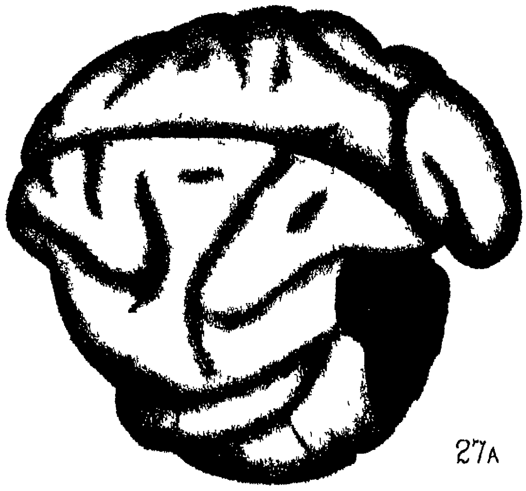
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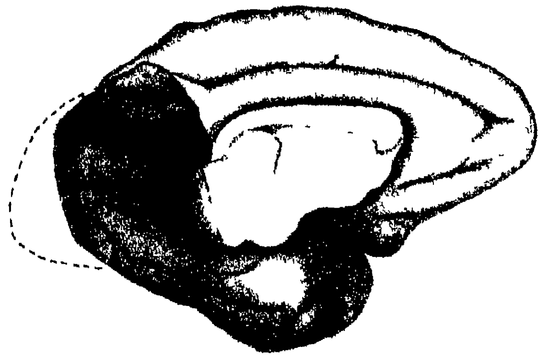
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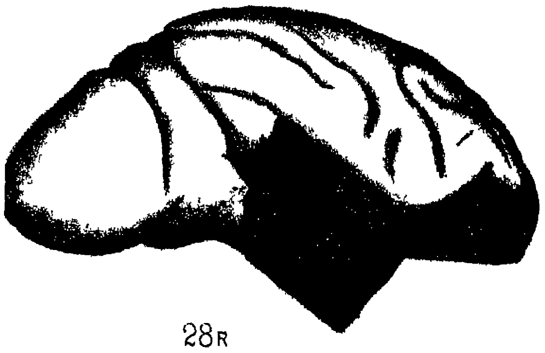
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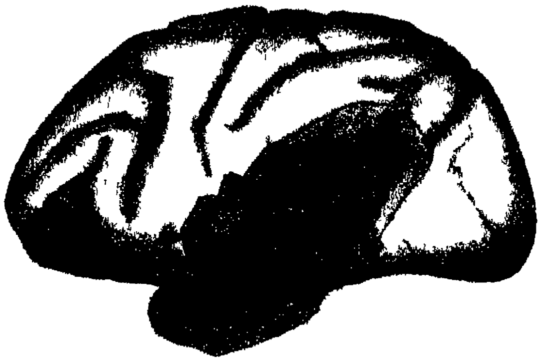
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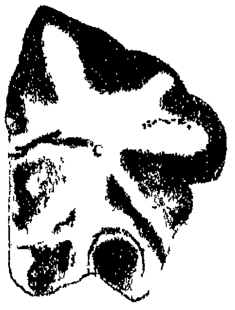
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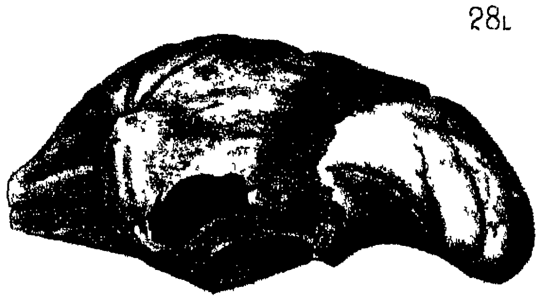
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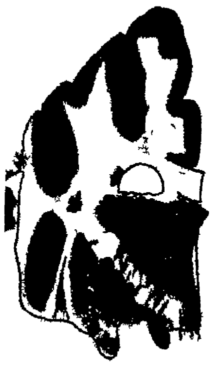
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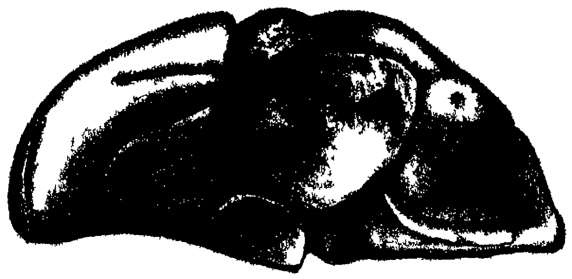
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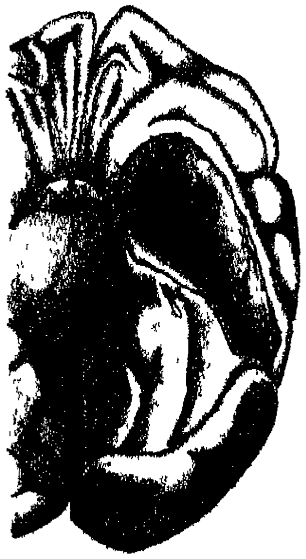
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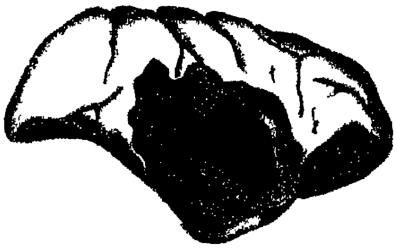
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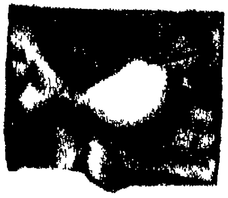
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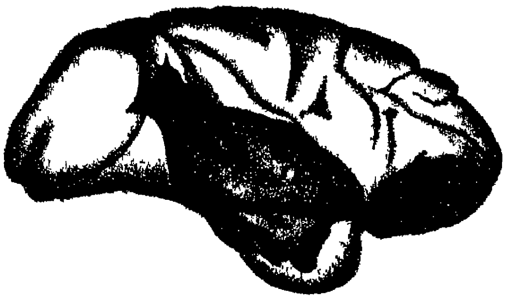
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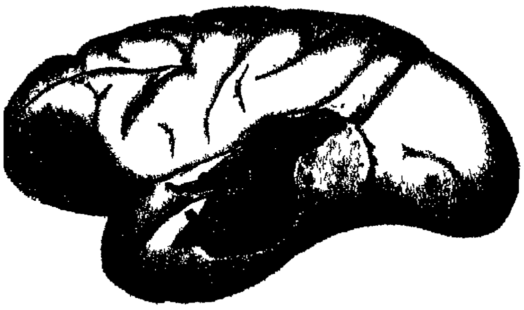
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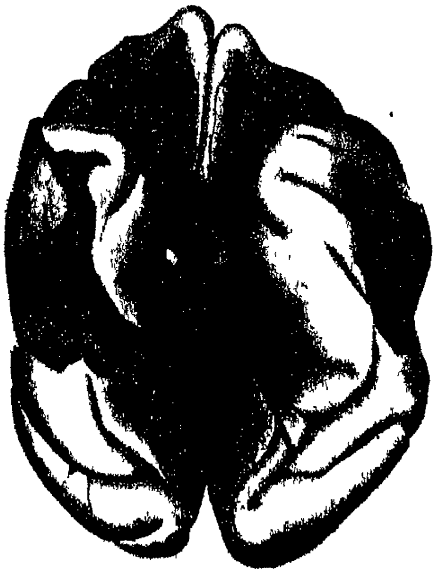
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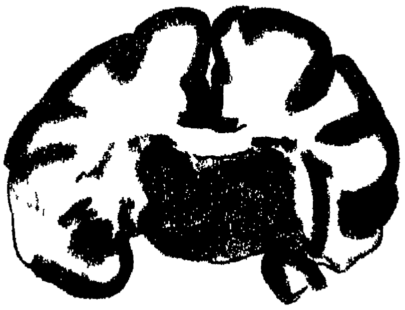
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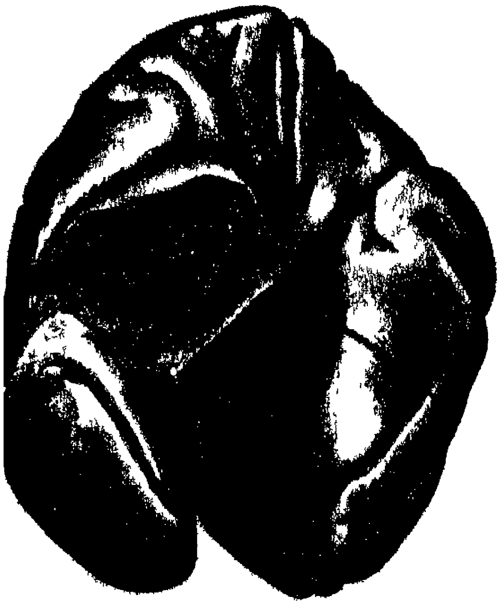
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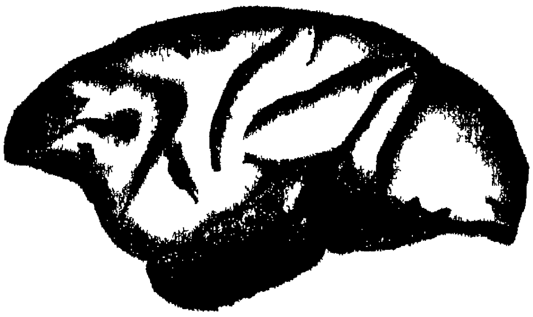
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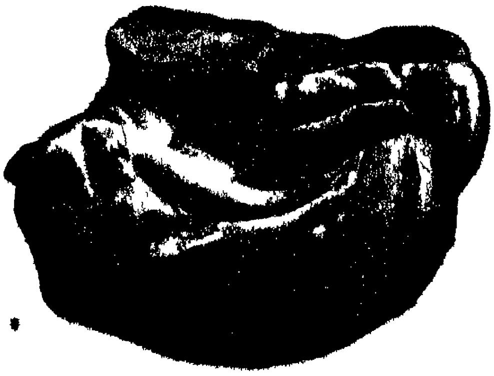
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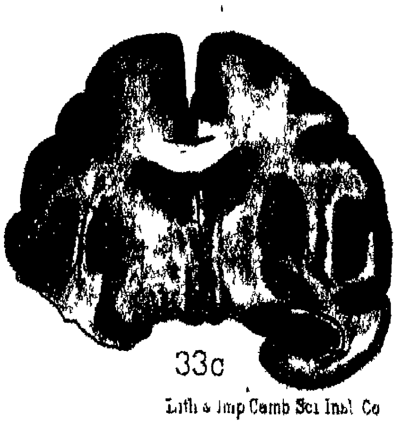
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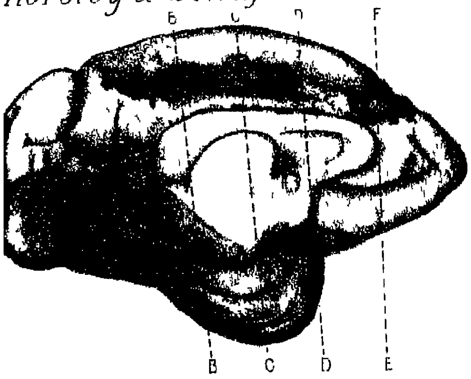

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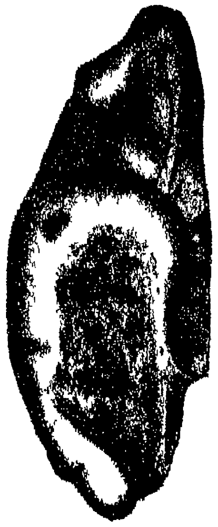

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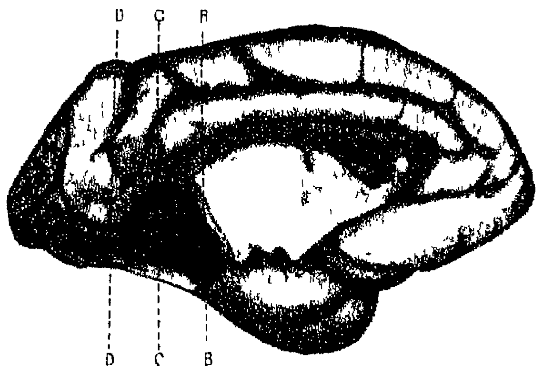

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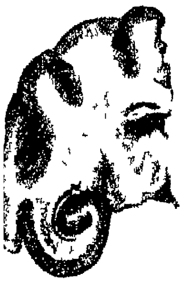

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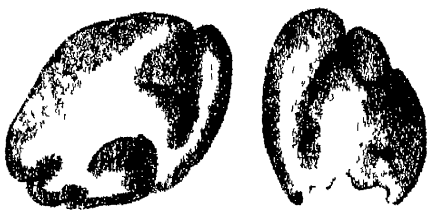

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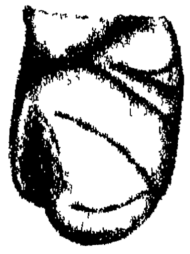

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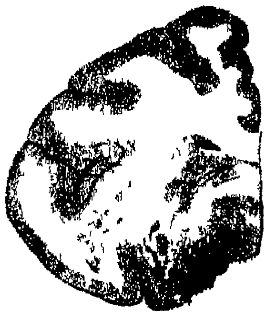

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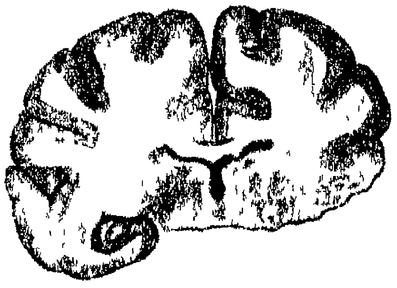

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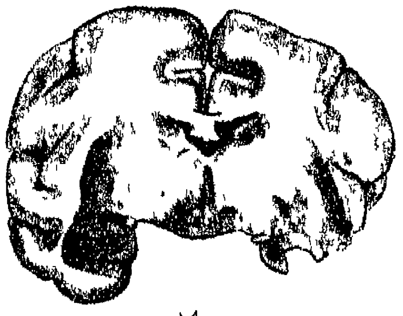

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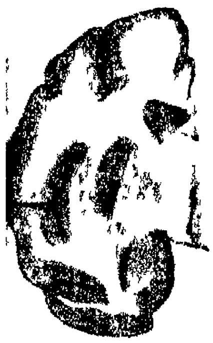

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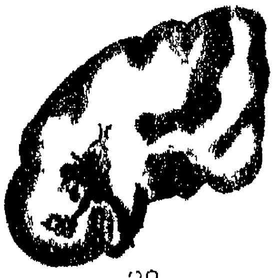

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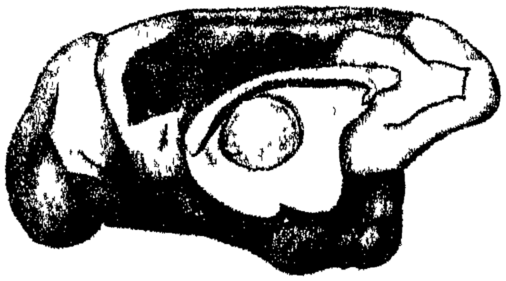

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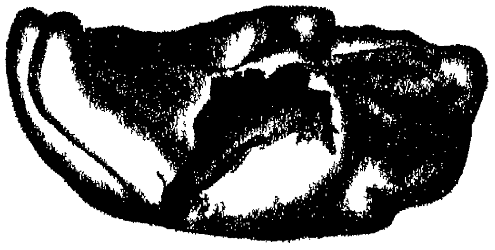

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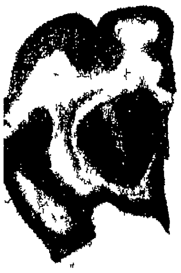

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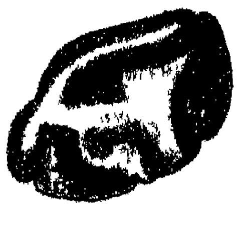

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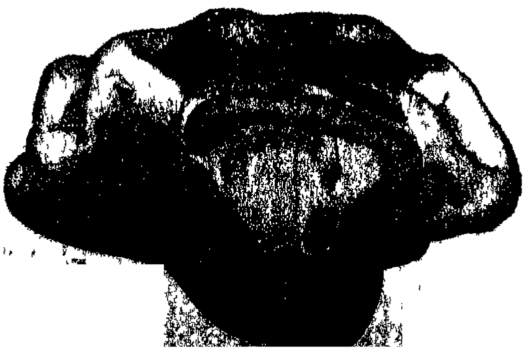

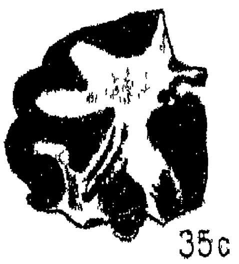

35C

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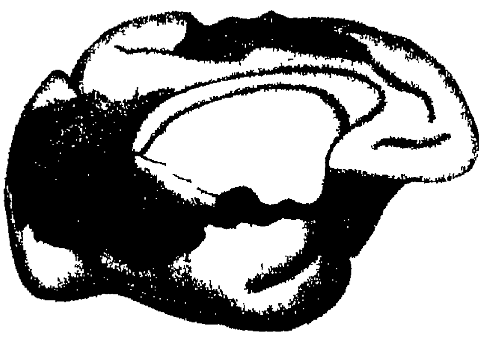
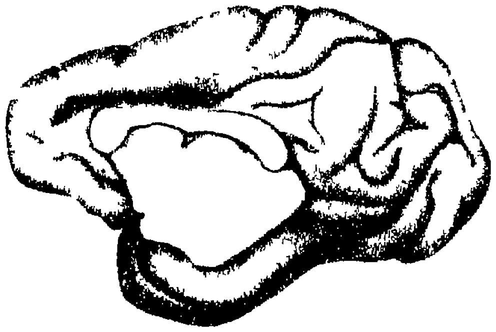
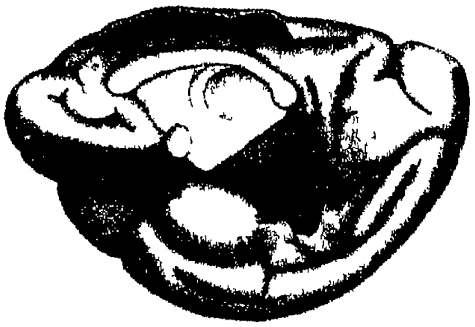
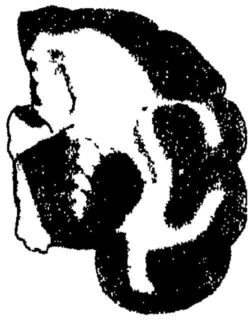
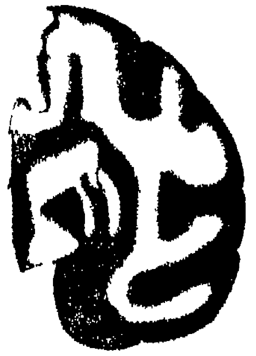
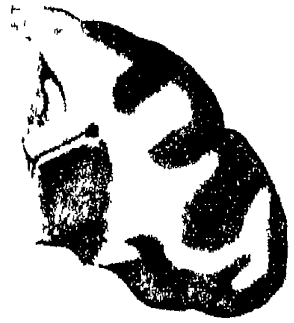
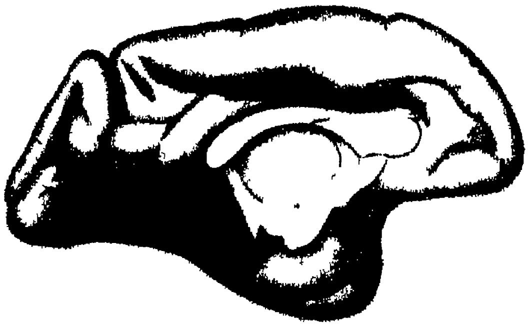
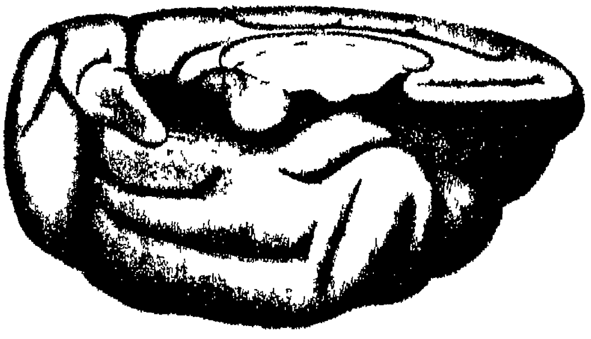

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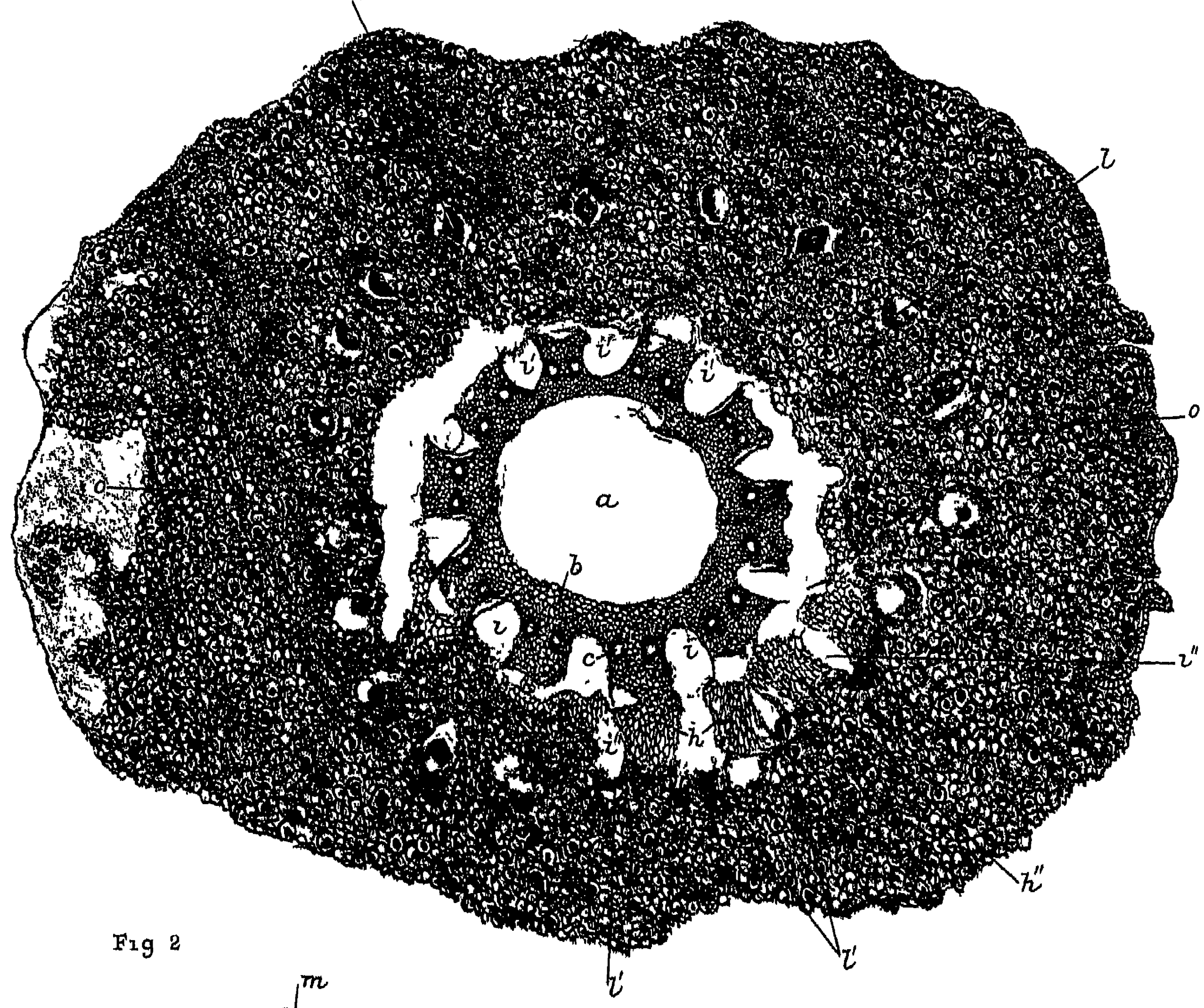
Fig 1



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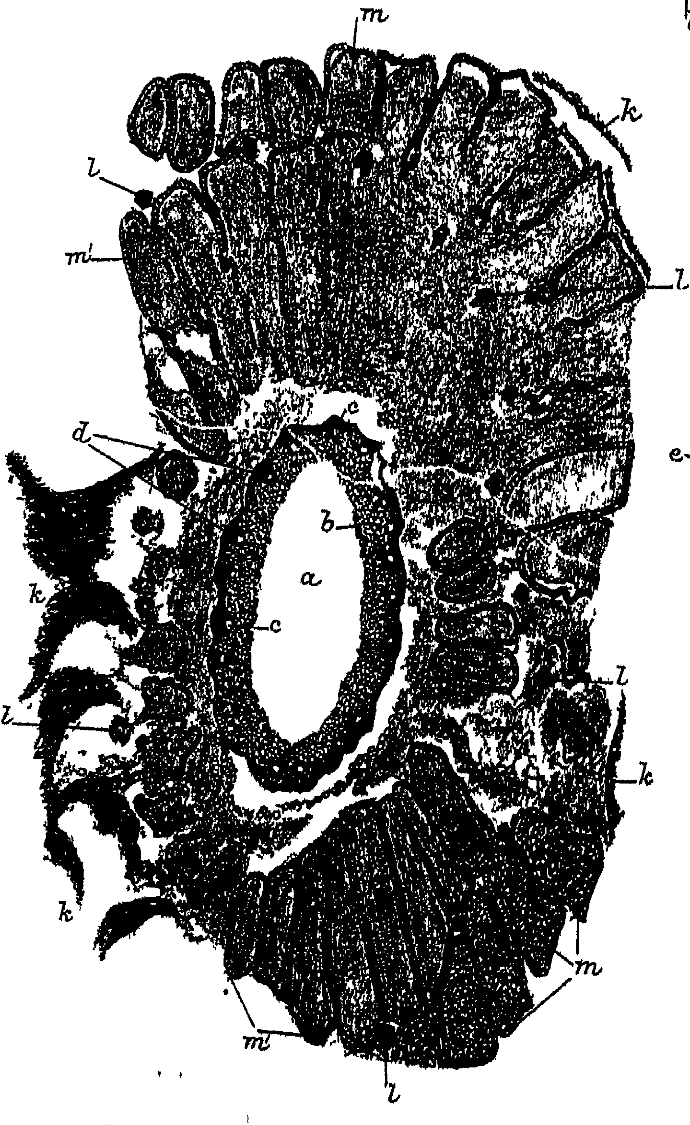

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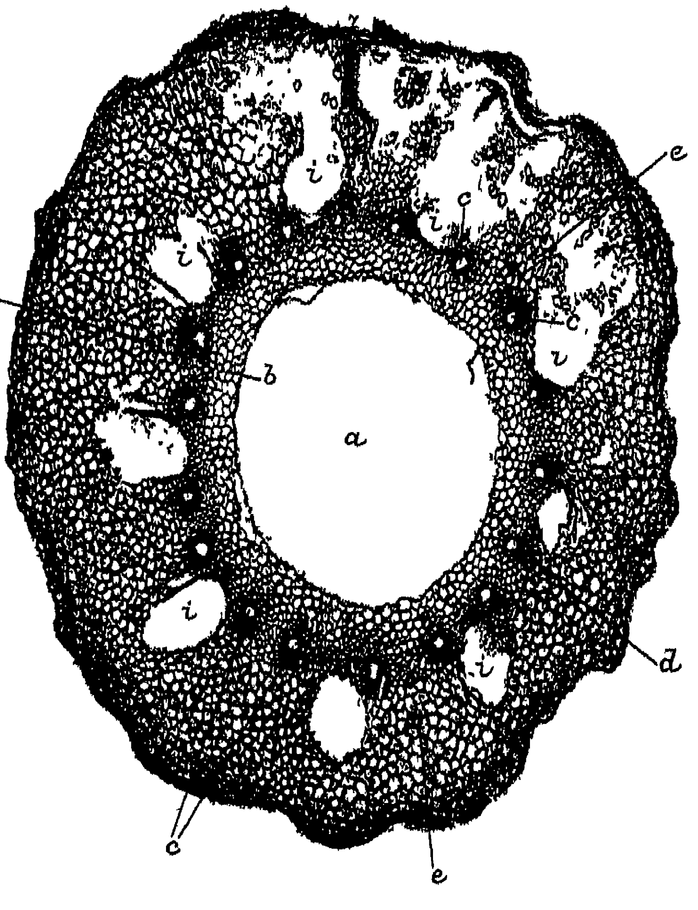

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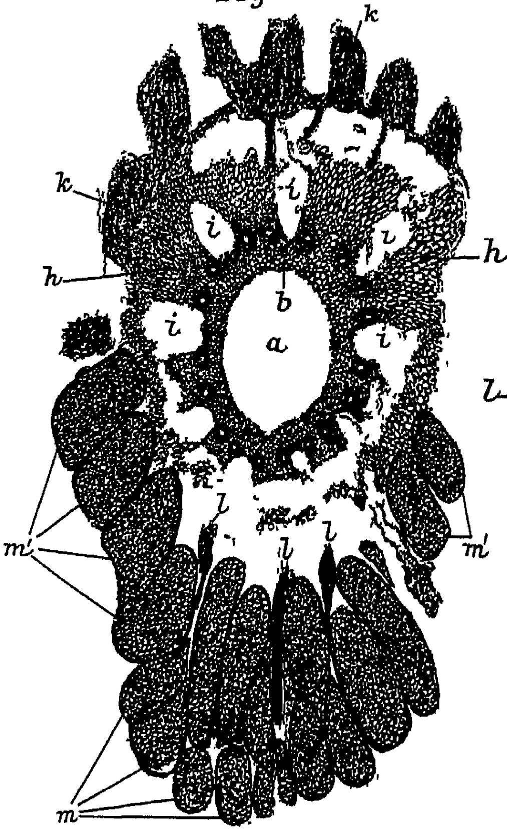
Fig 3



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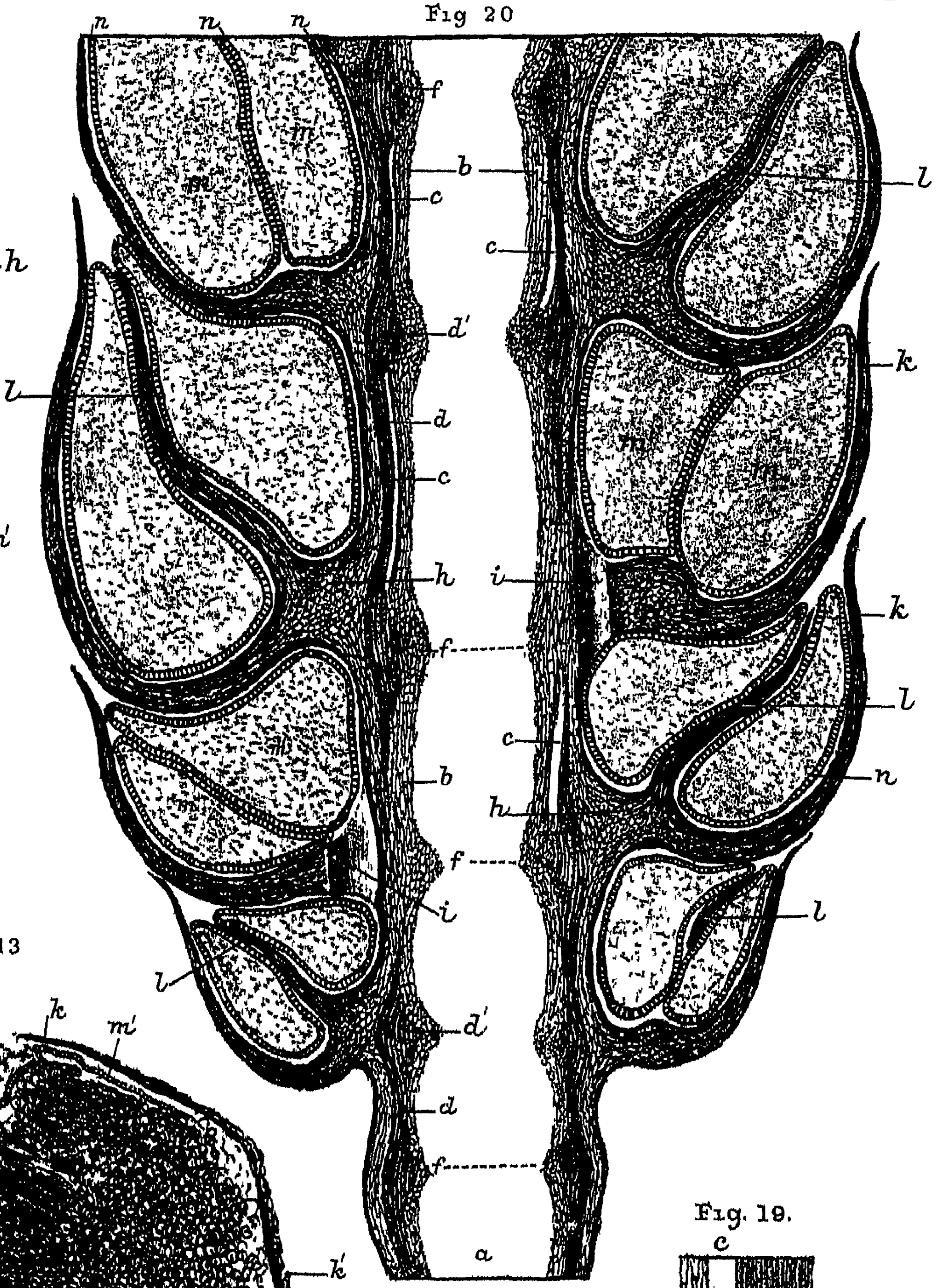

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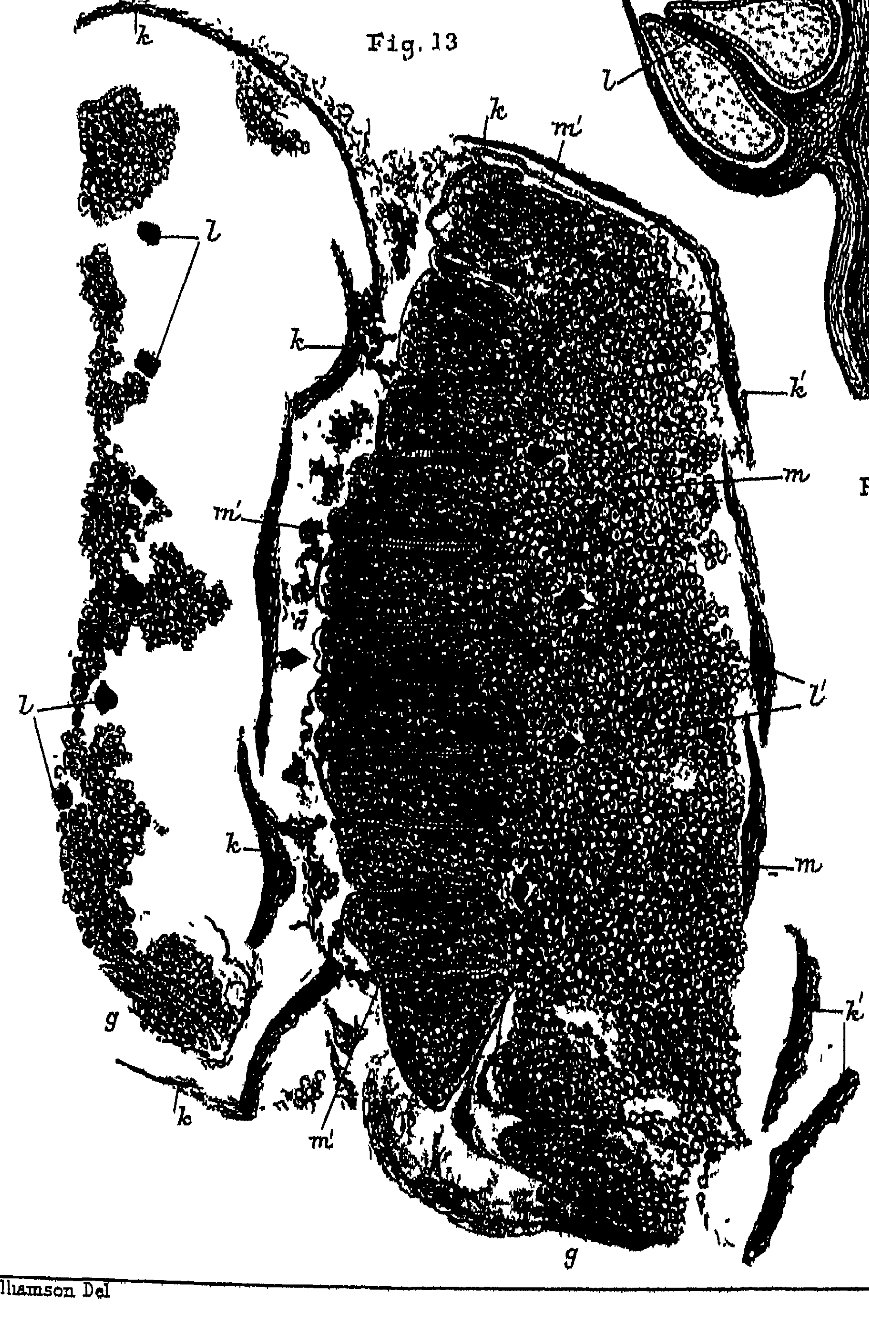

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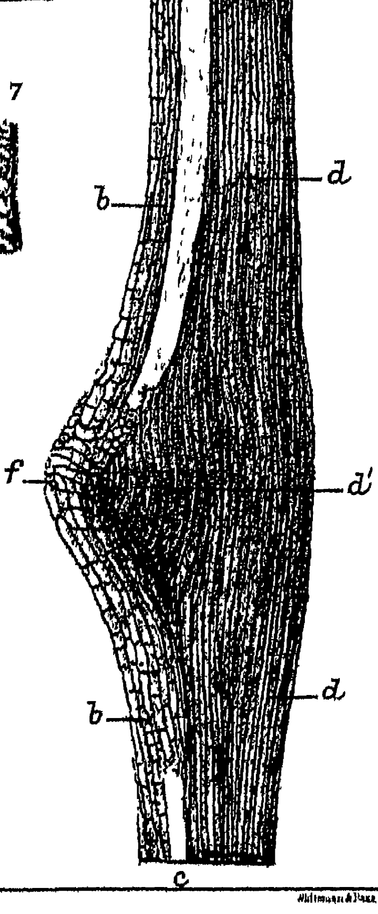

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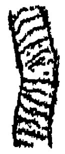

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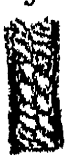

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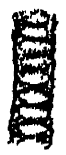

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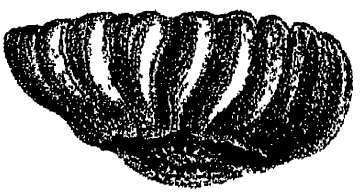

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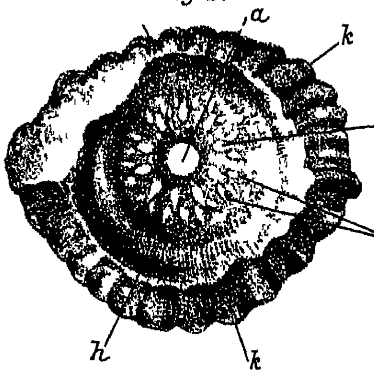

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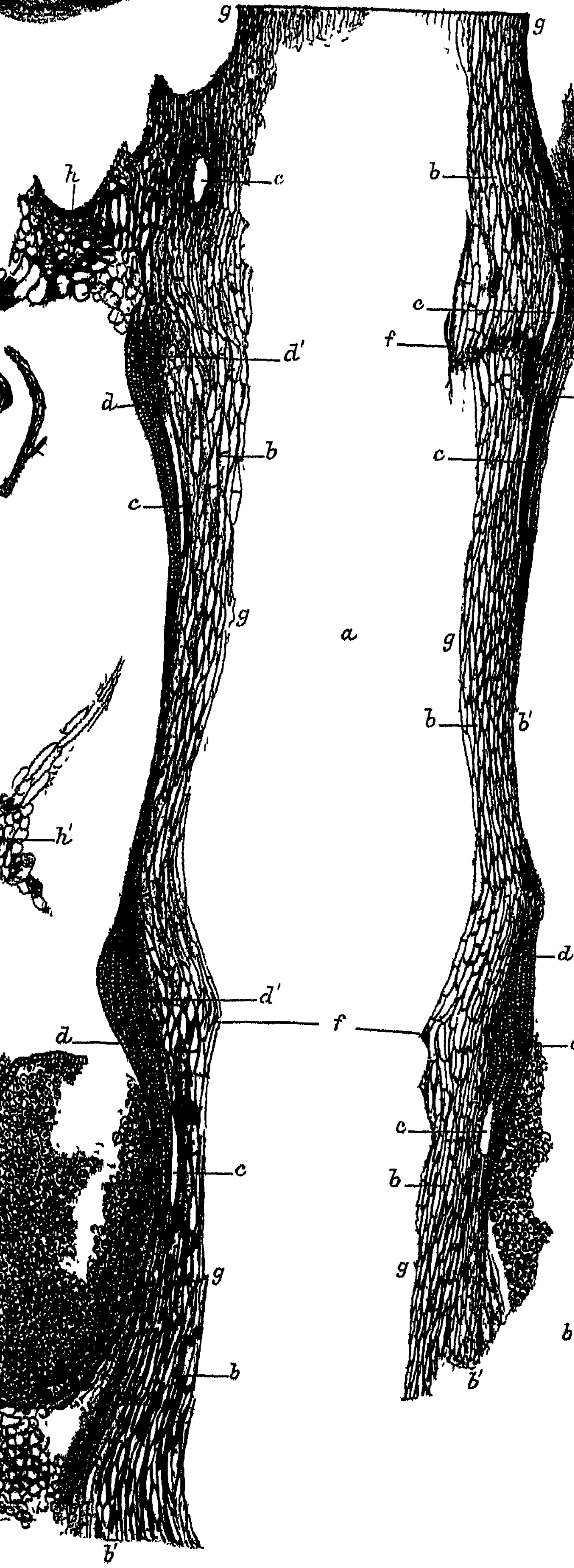

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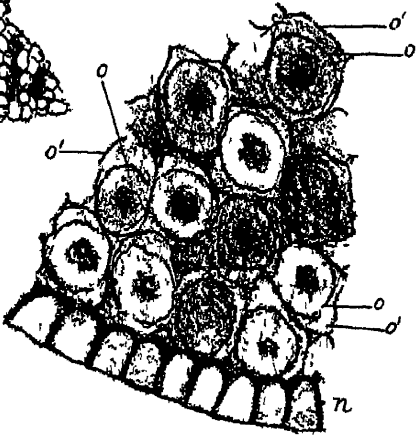

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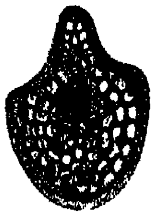

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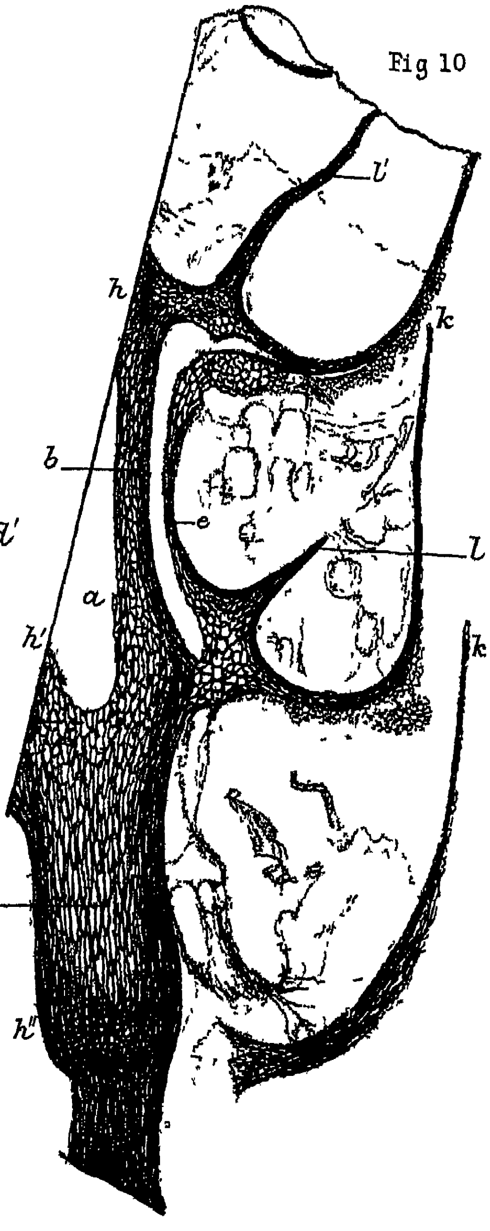

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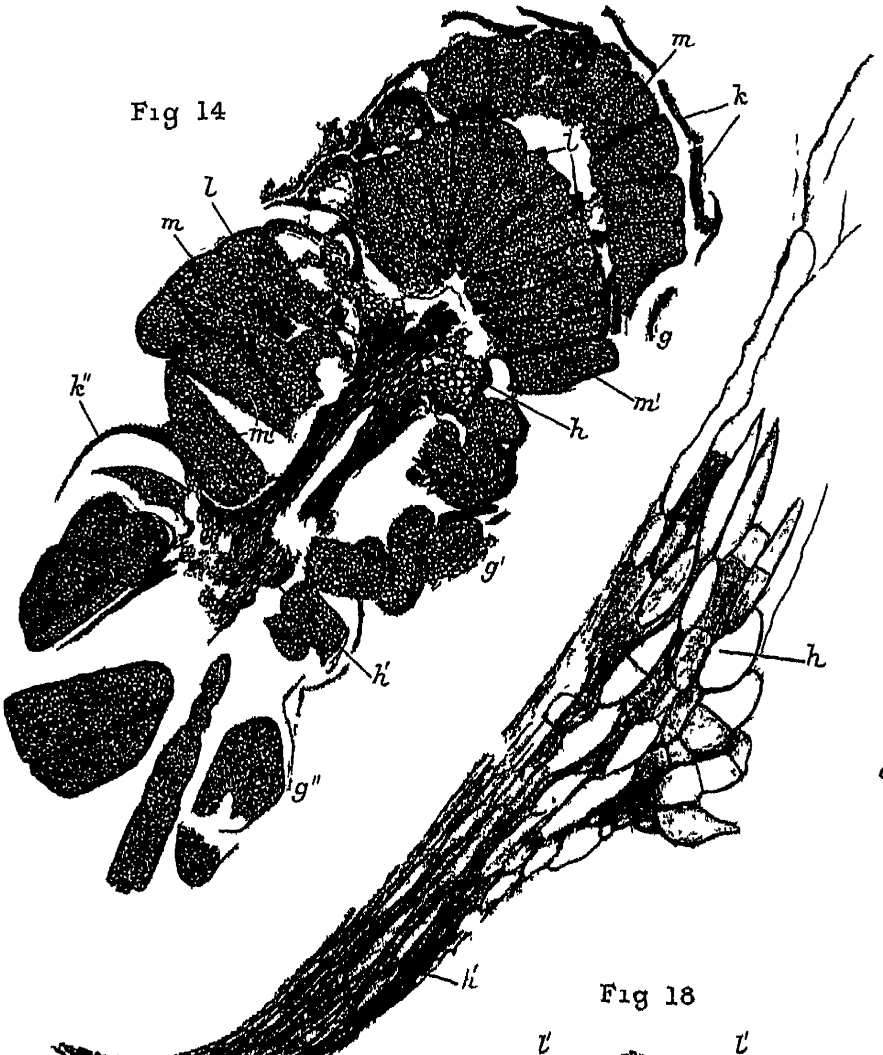
Fig 14



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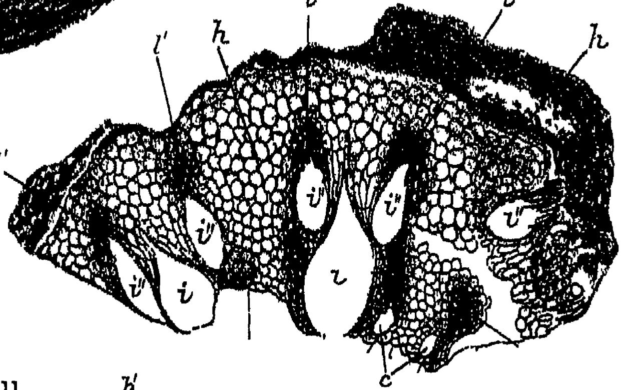

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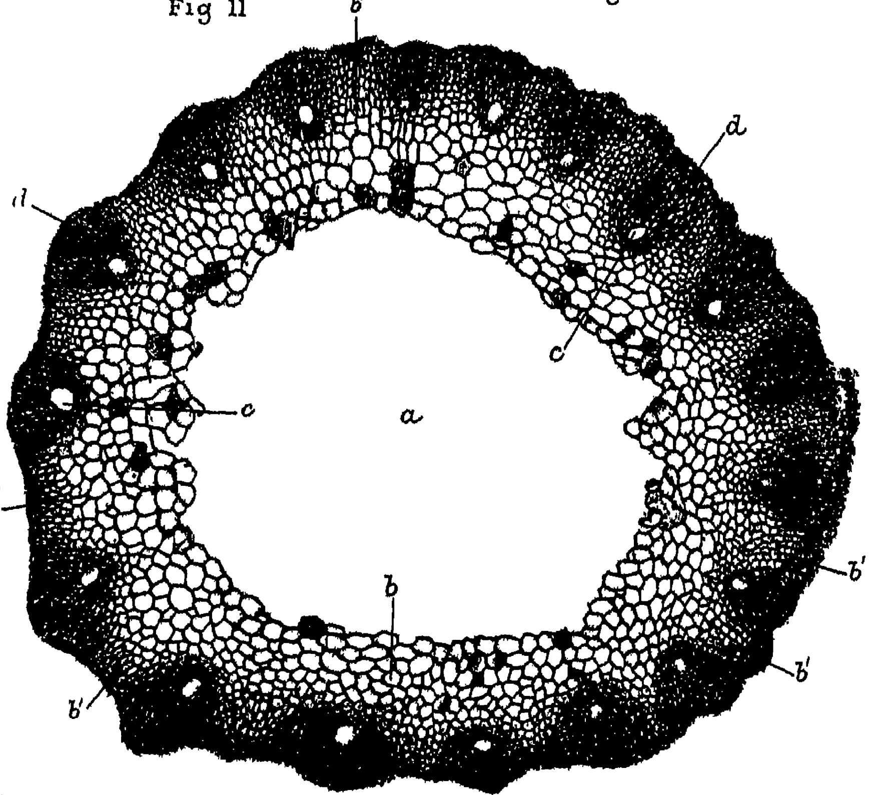

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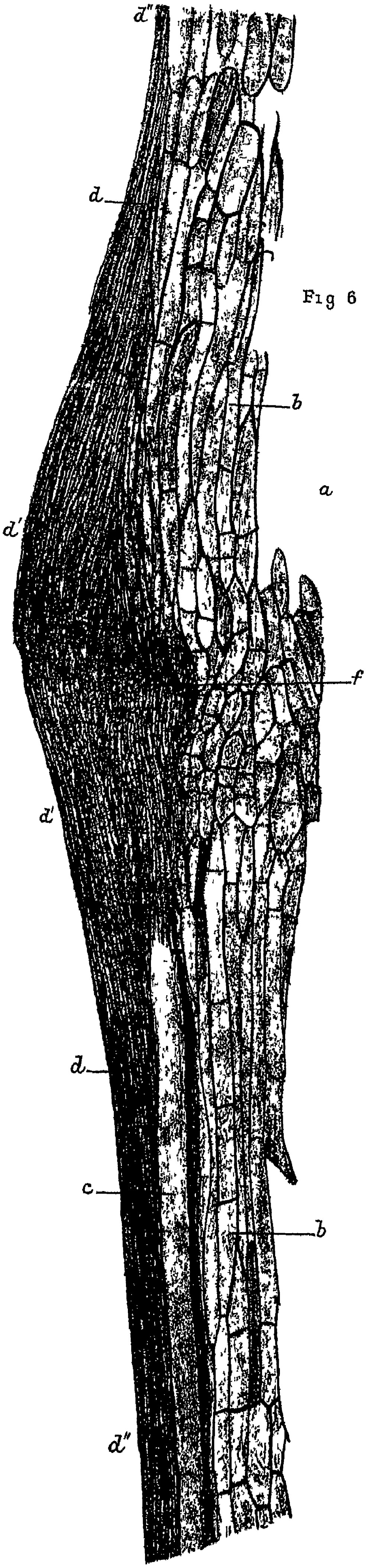

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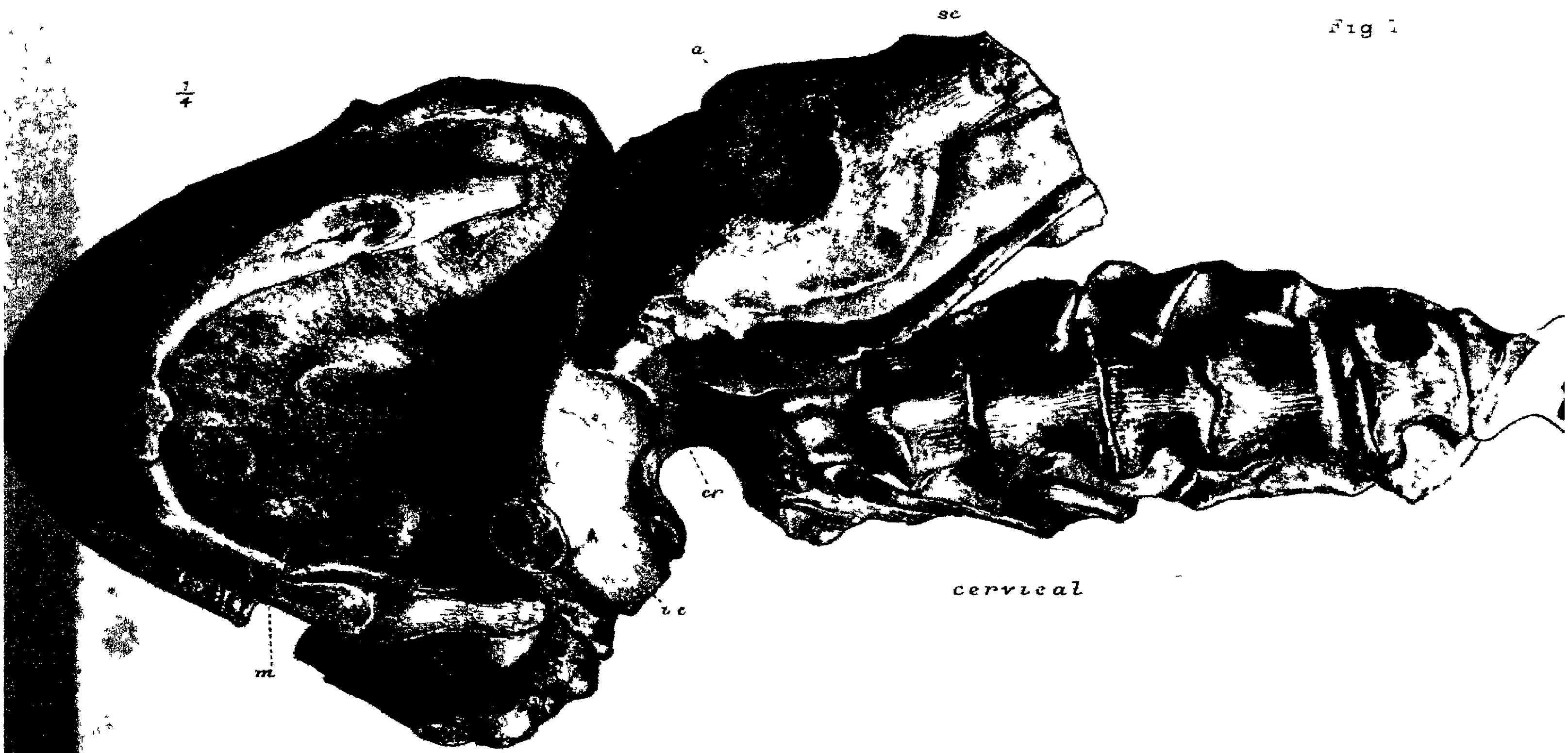

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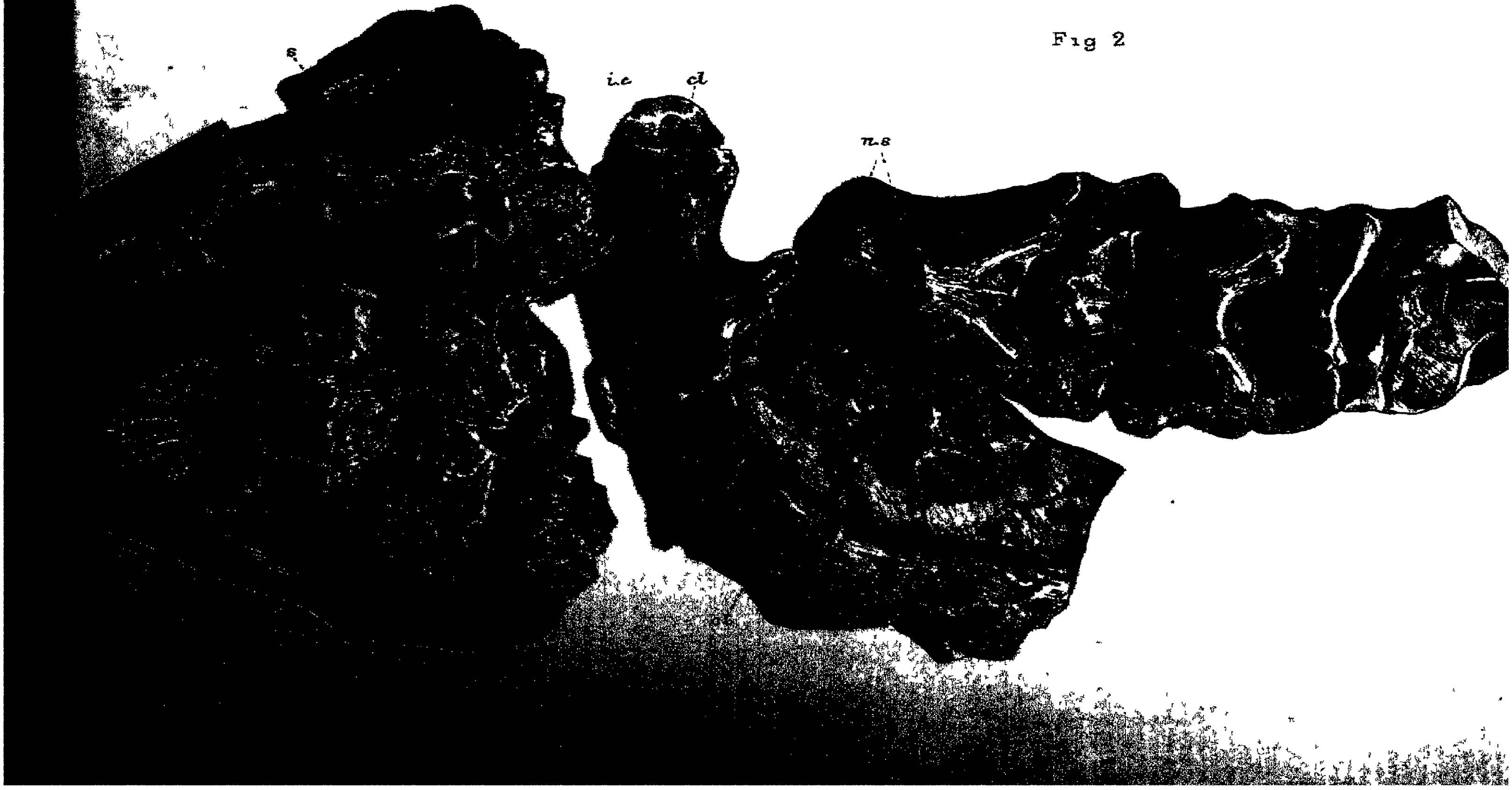

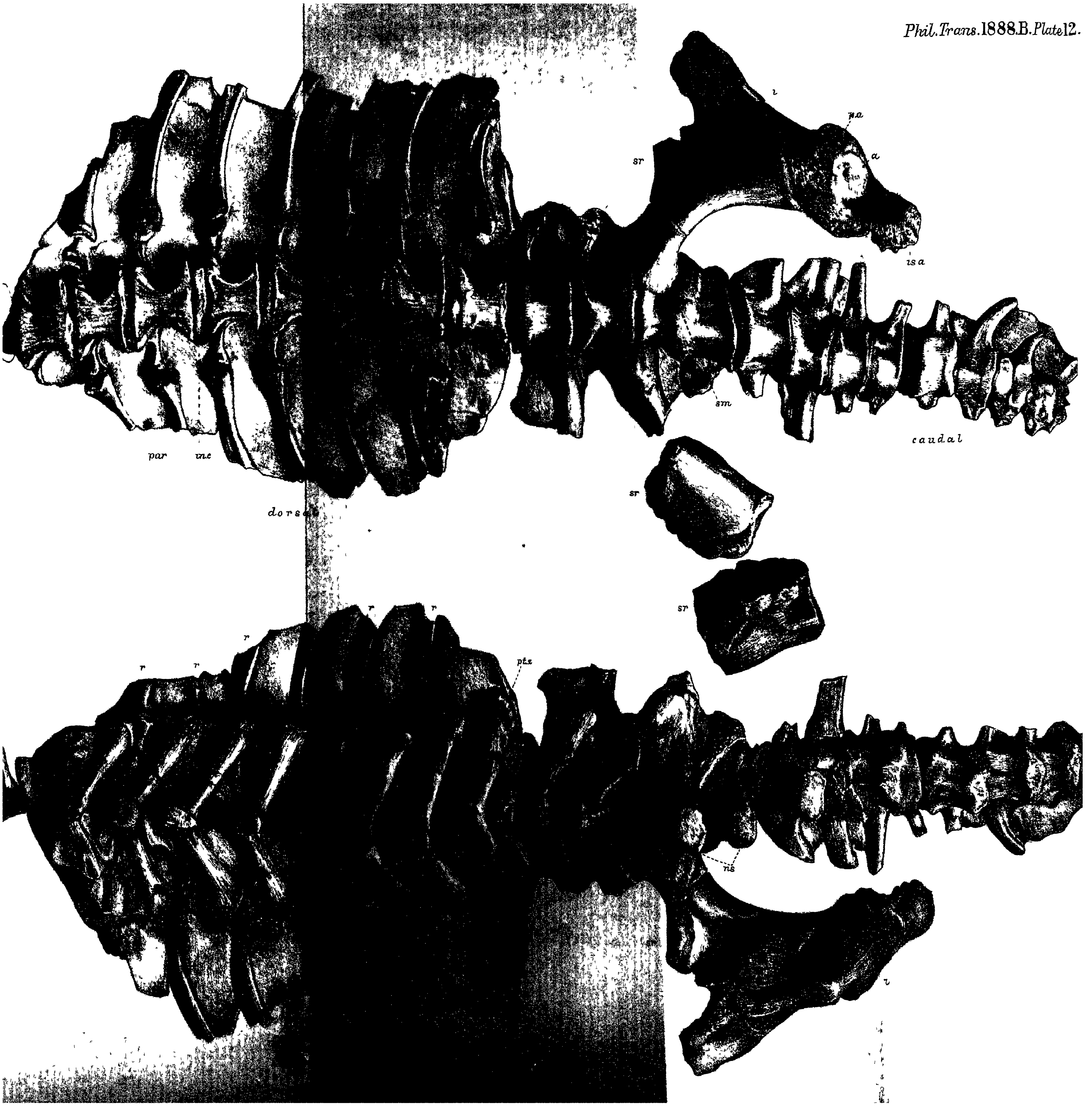
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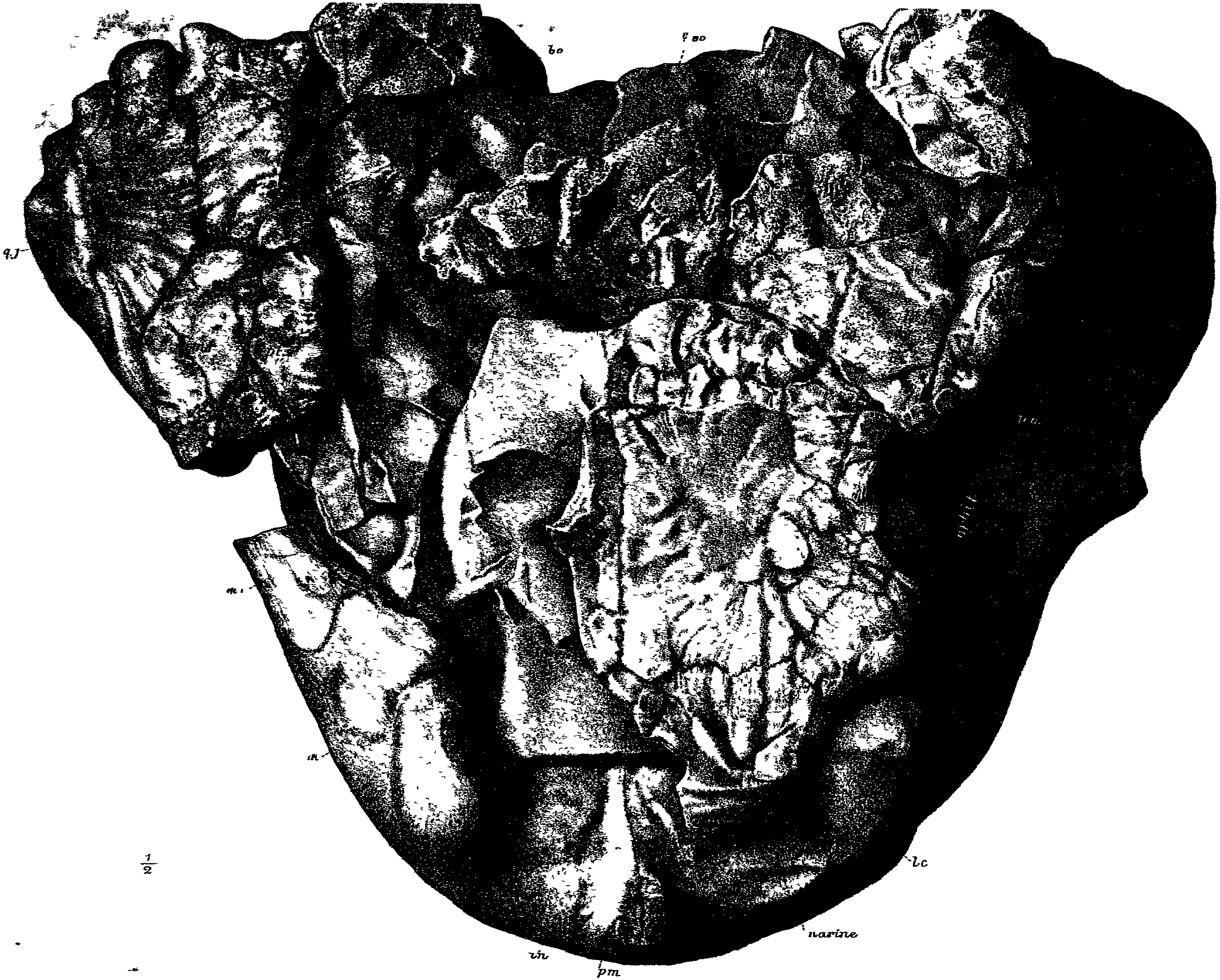

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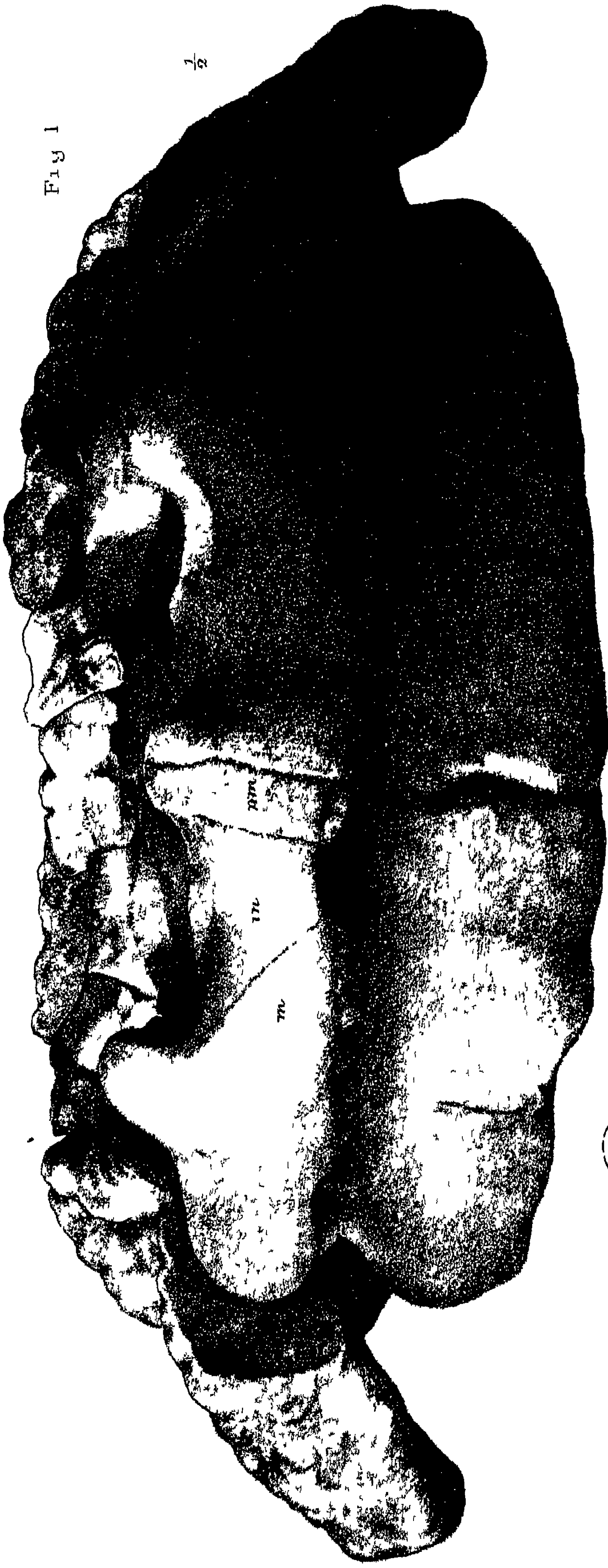
West, Newman & Co. imp

Fig 1



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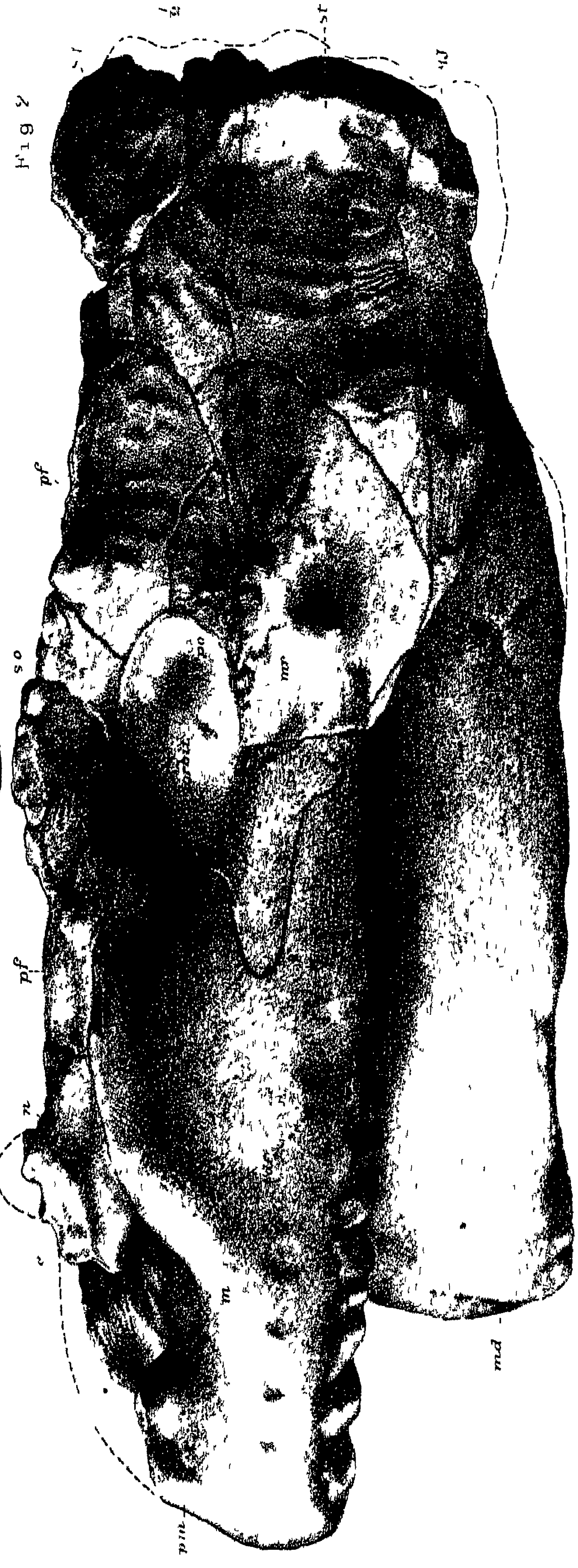
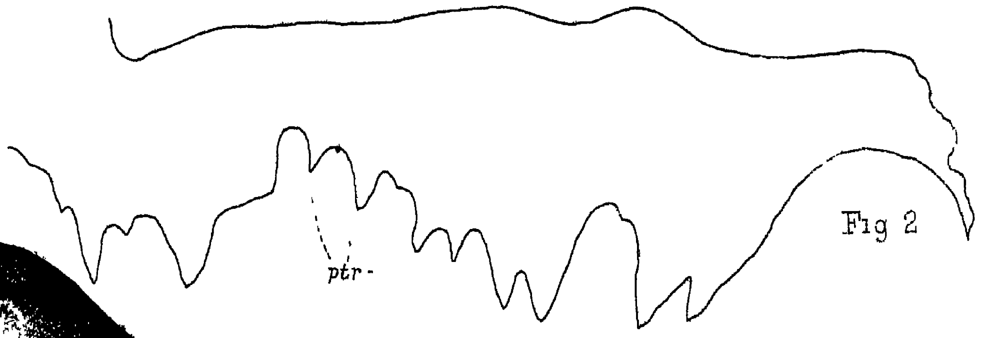


West, Newman & Co imp.



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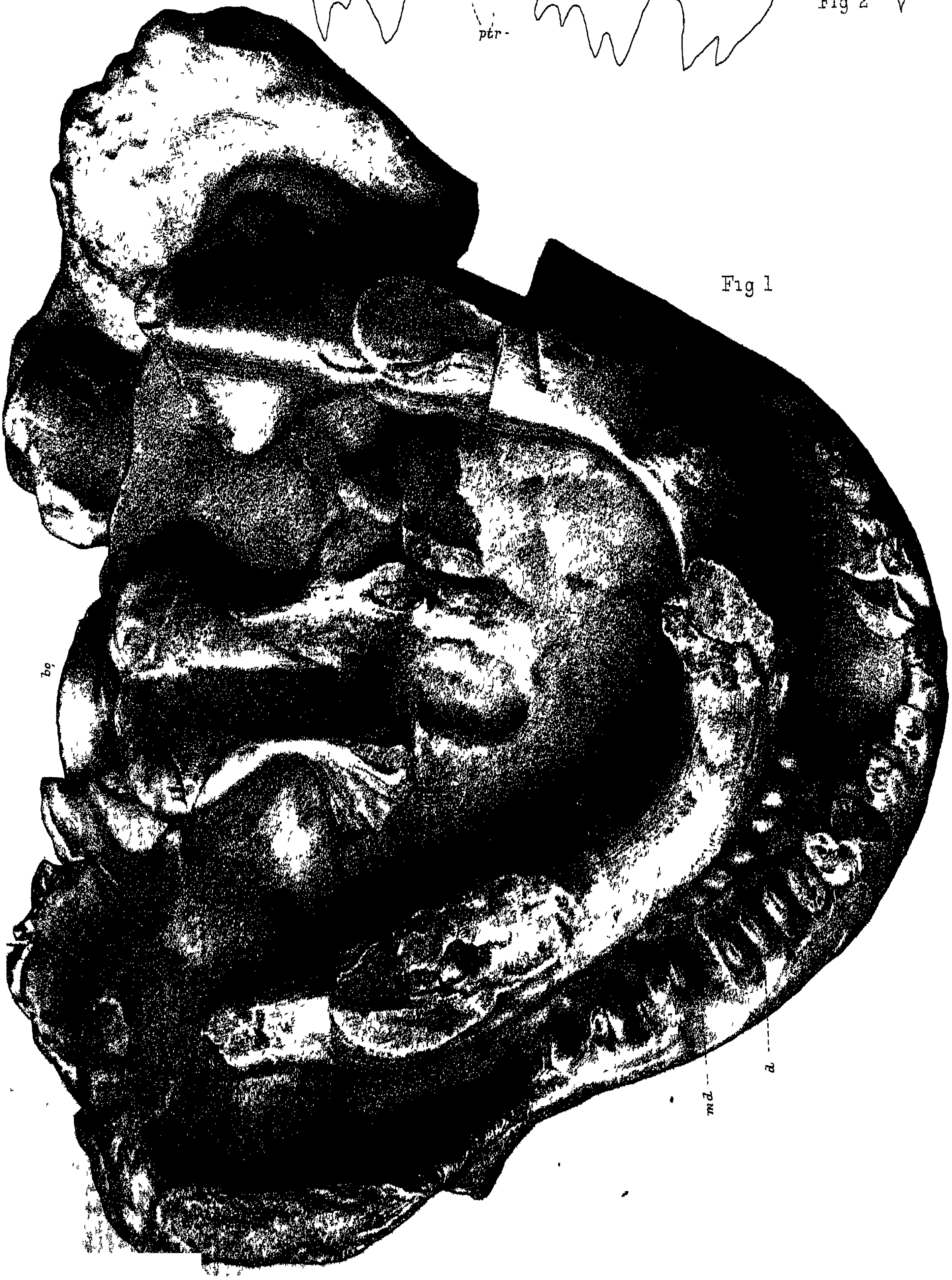

Fig 1

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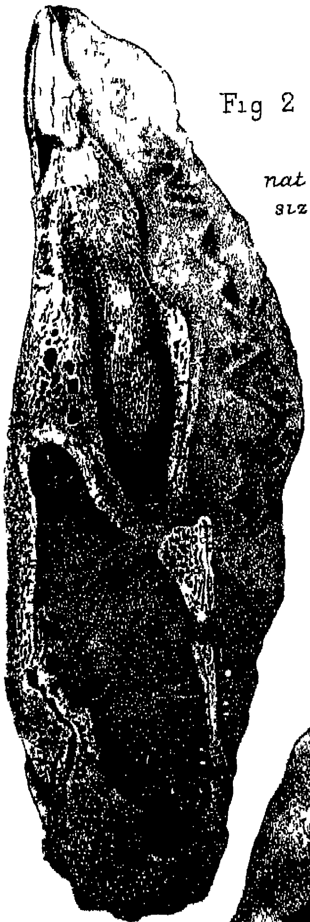

Fig 2

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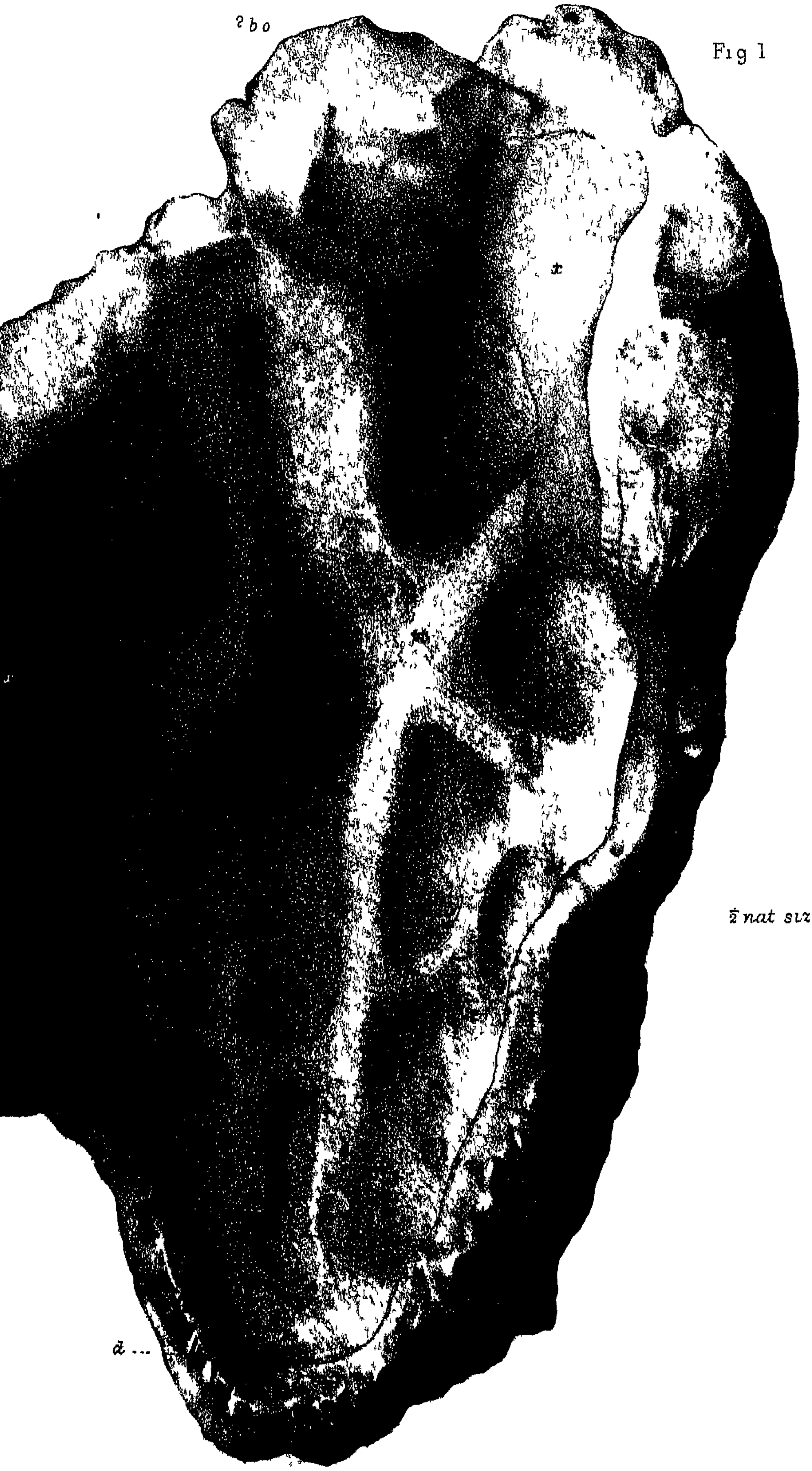

Fig 1

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West Newman & Co imp

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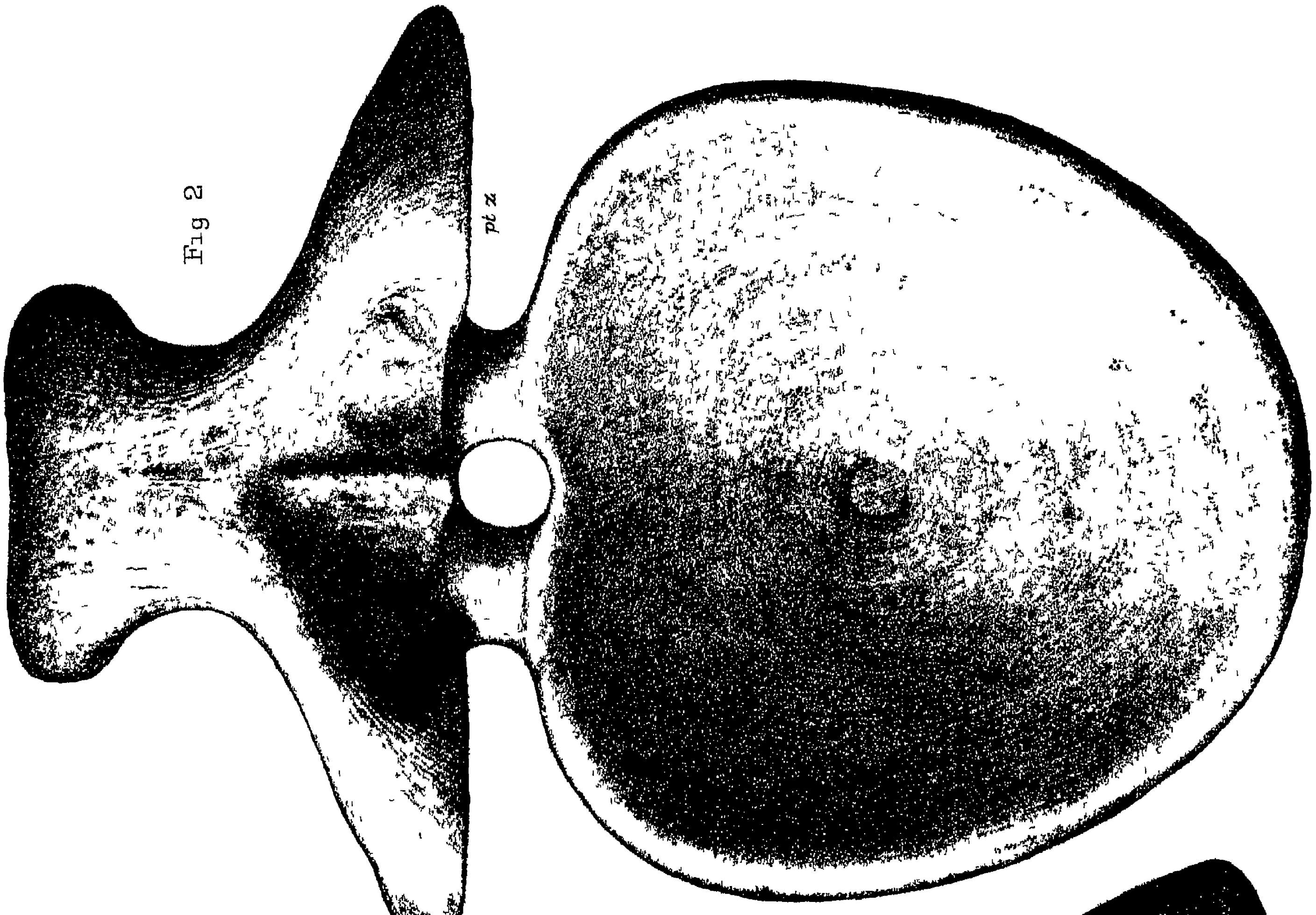
Fig 2



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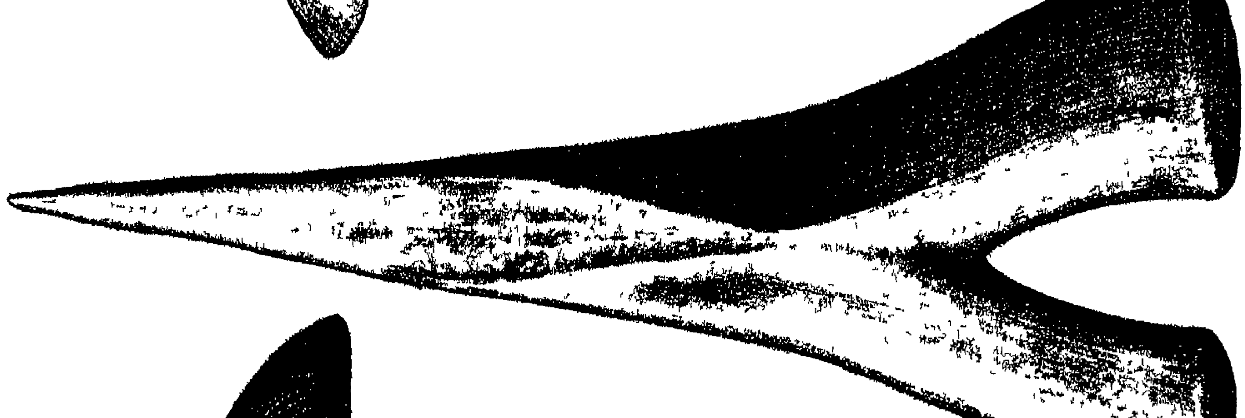

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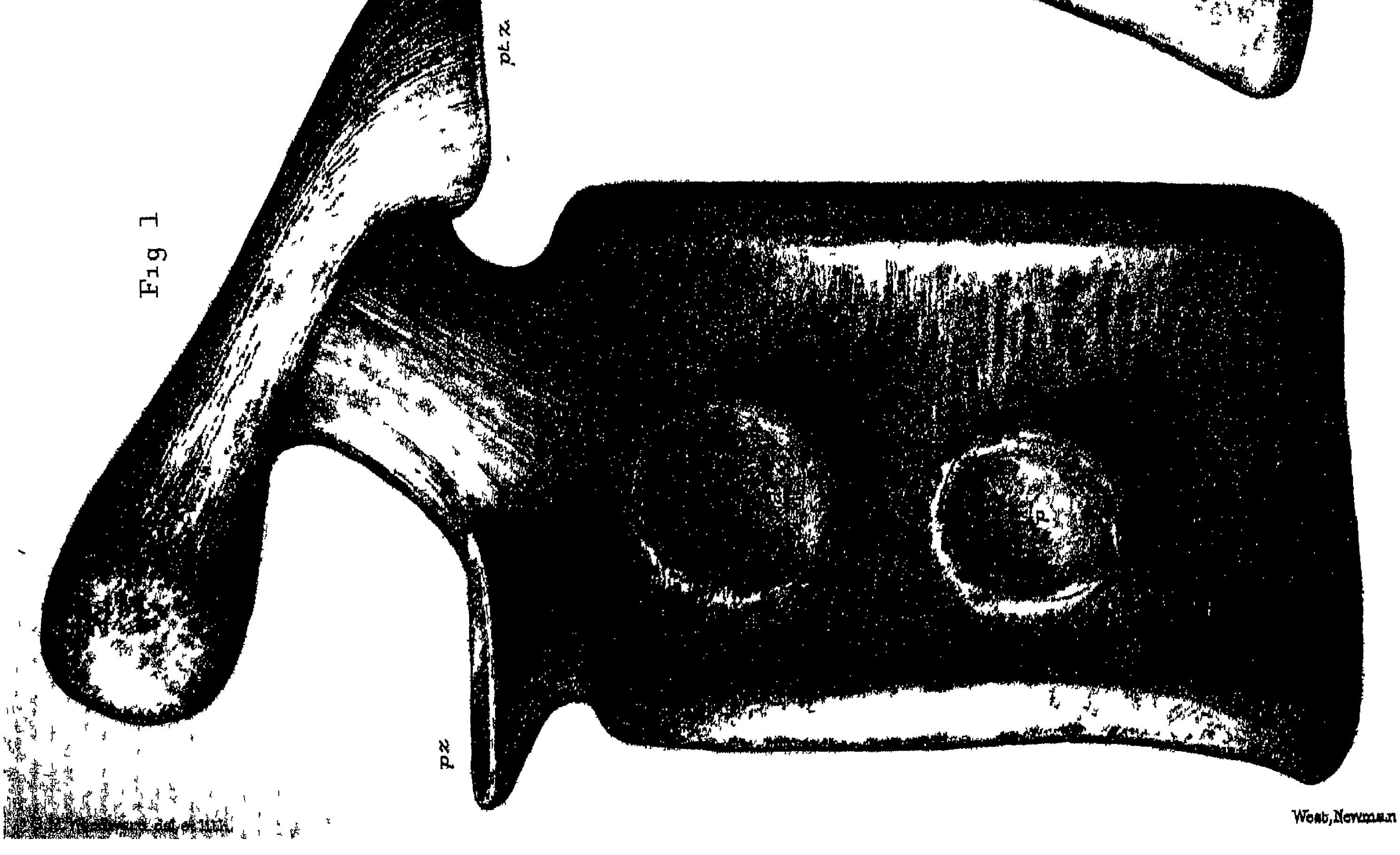
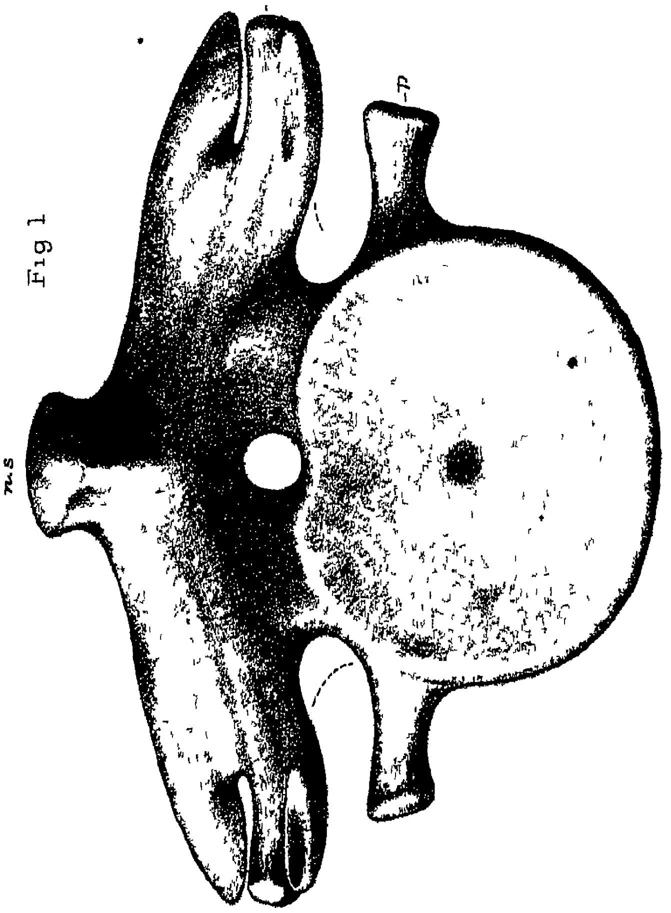


West, Newman & Co imp.

Fig 1



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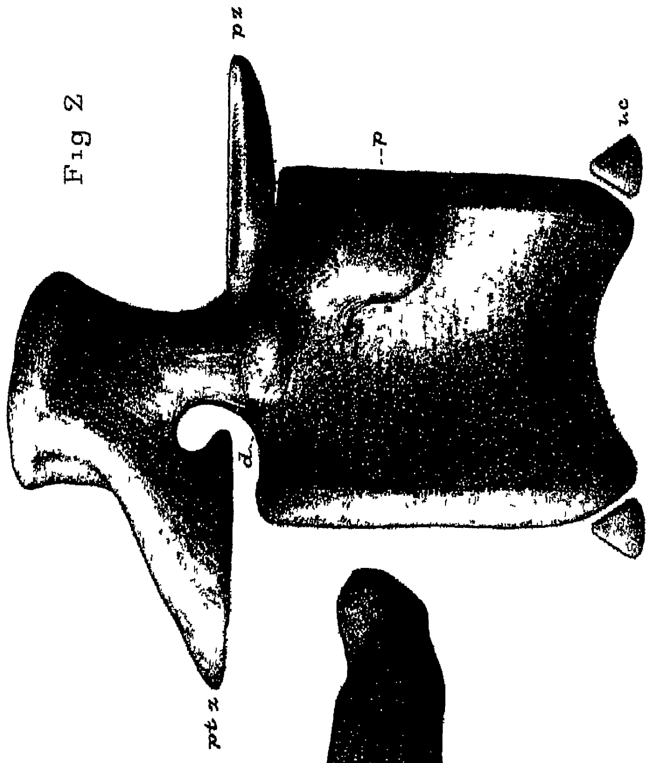

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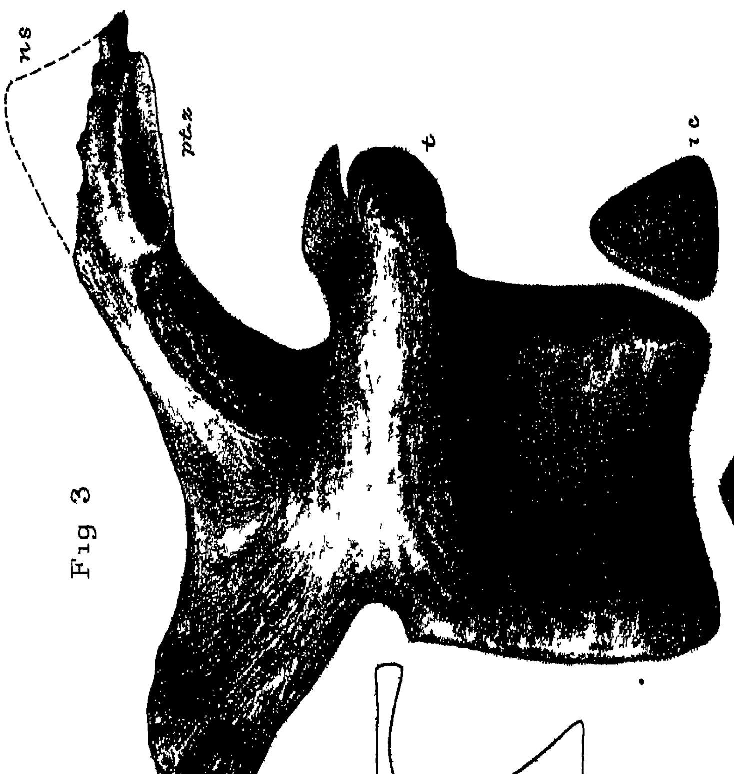

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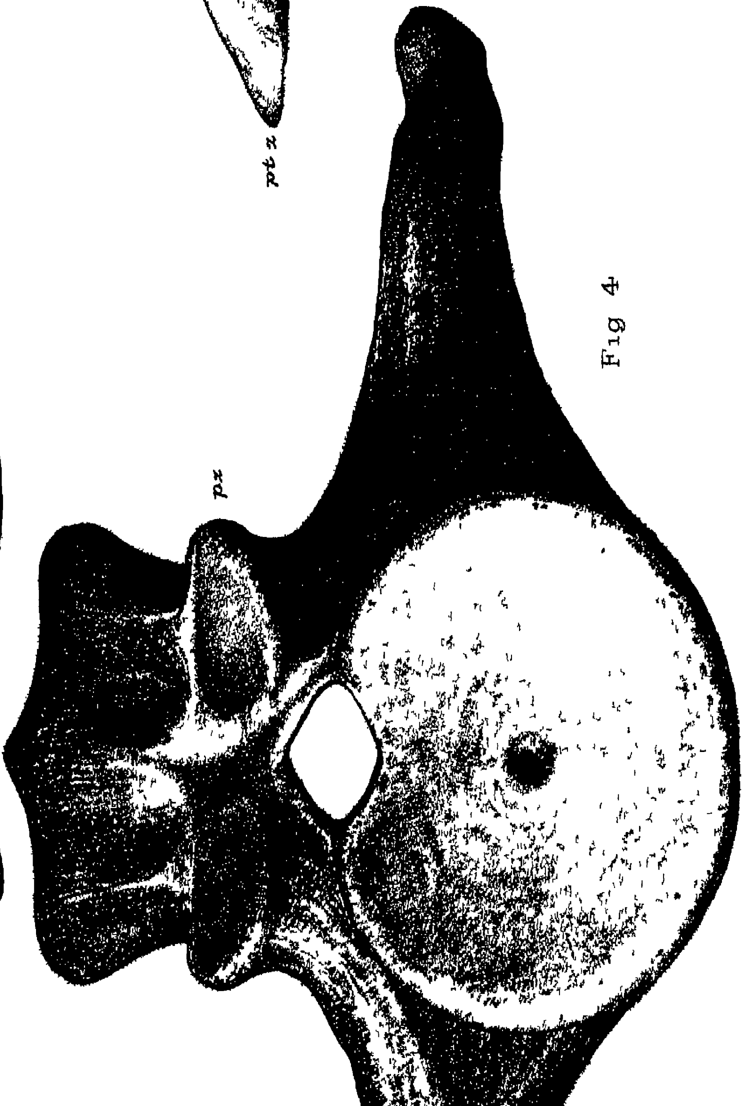

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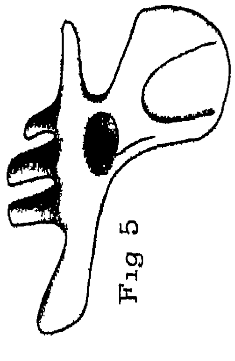

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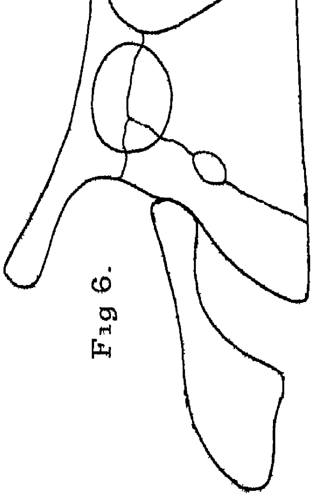

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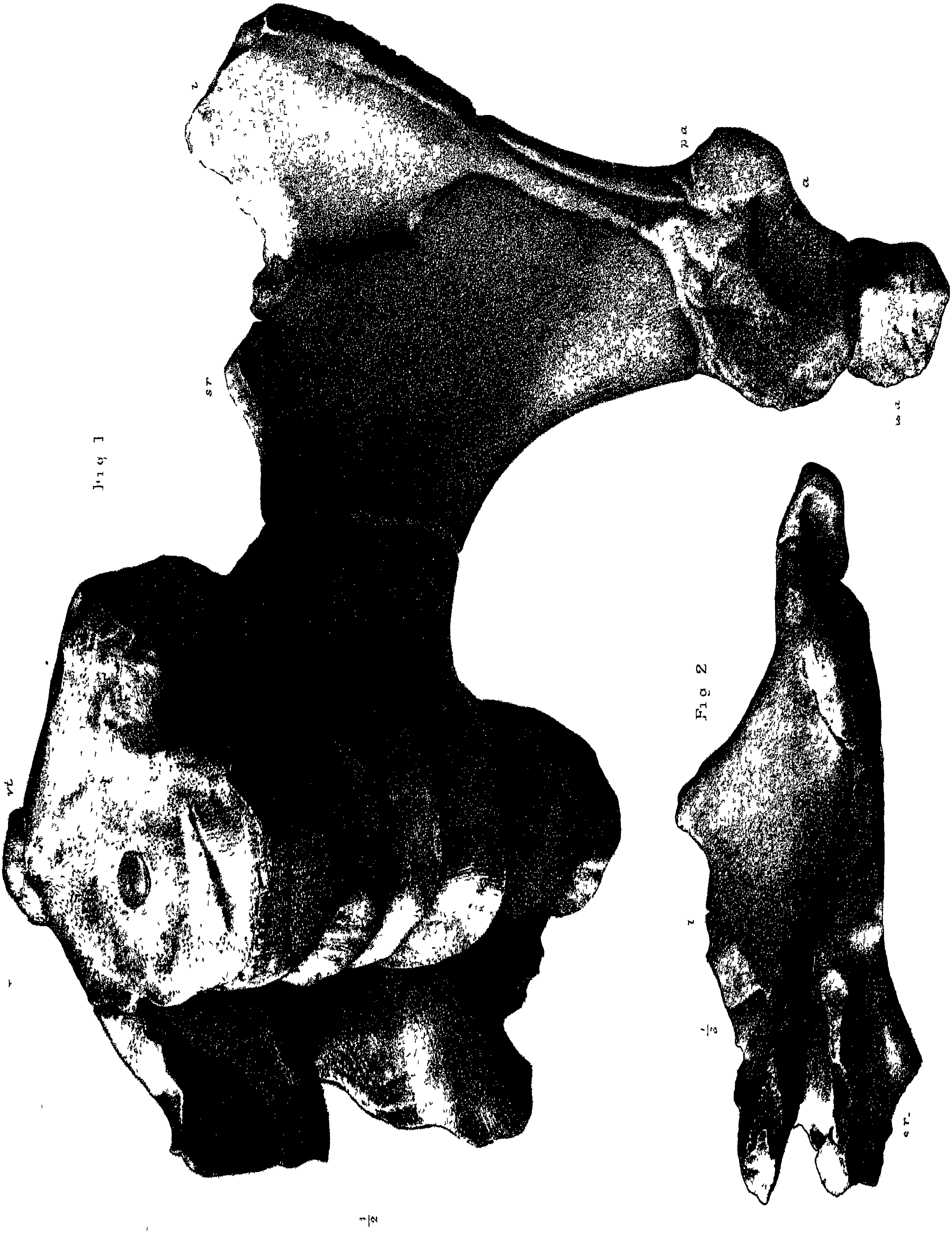

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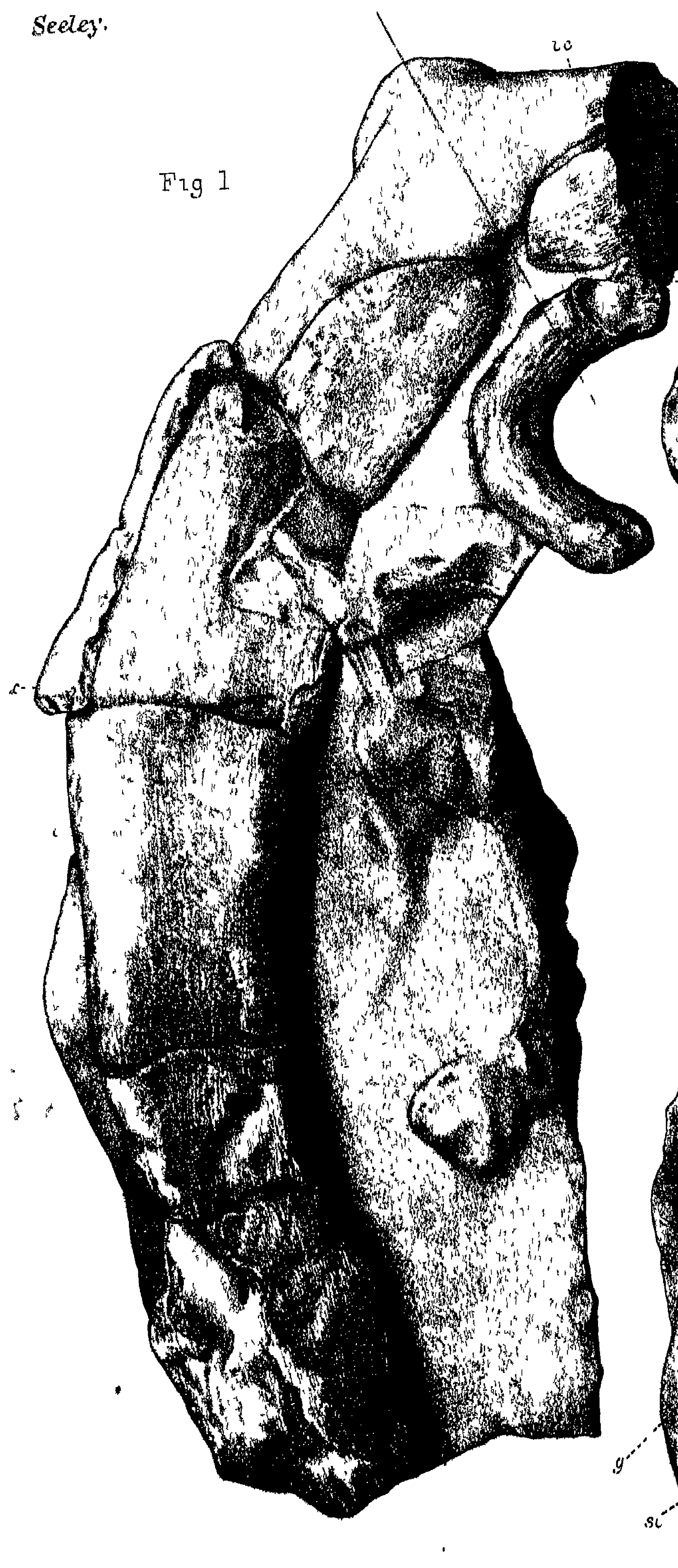
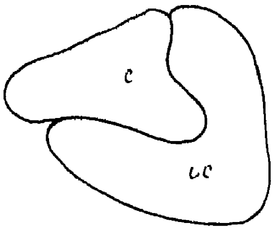


Fig 1



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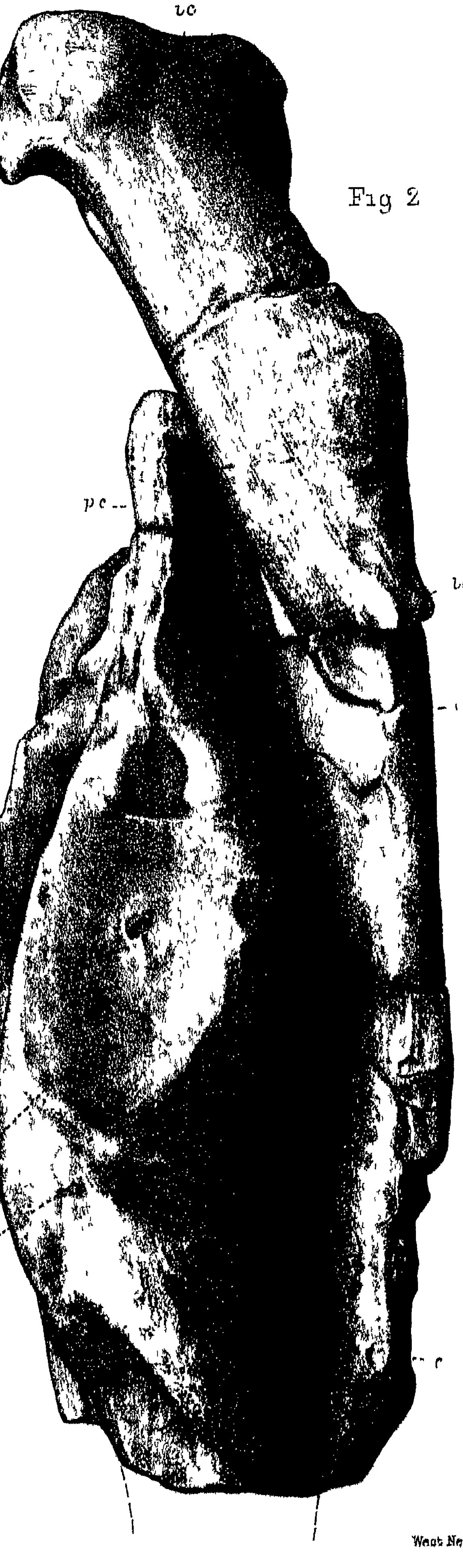

Fig 2

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Fig 3

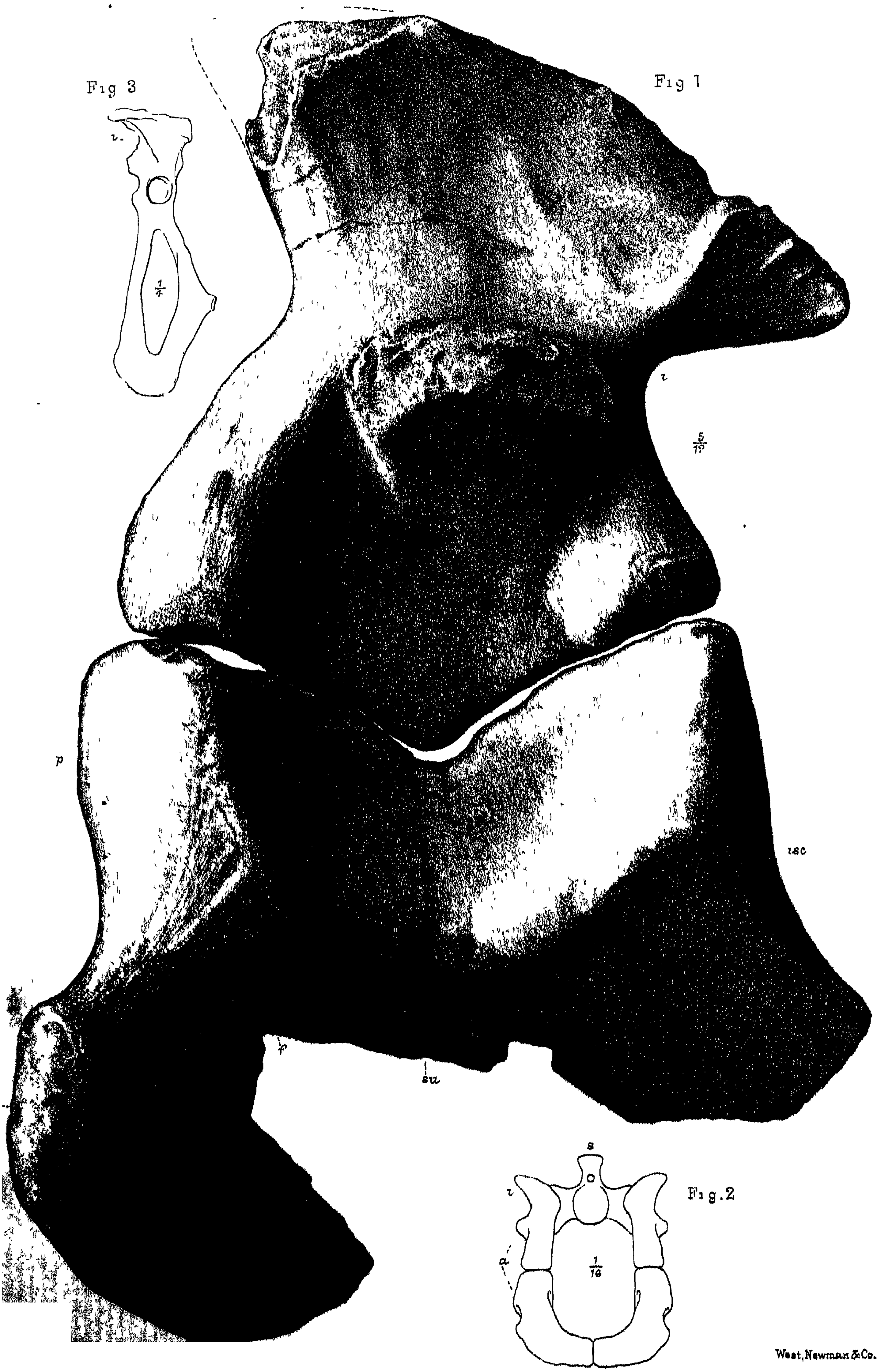

Fig 1

Fig. 2

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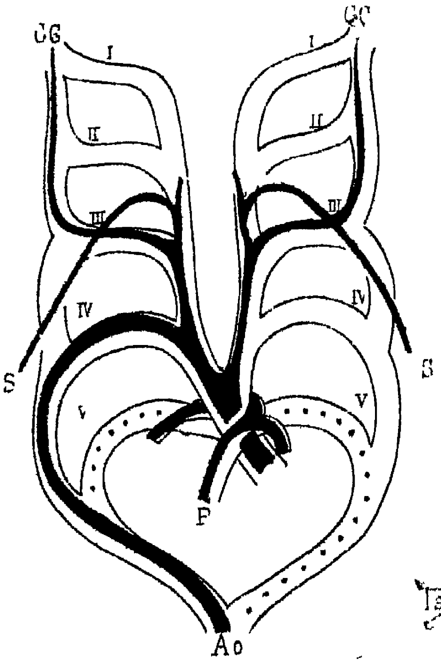
Fig 2



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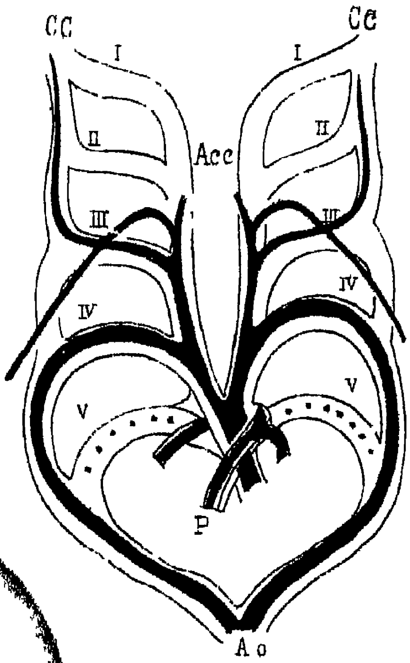
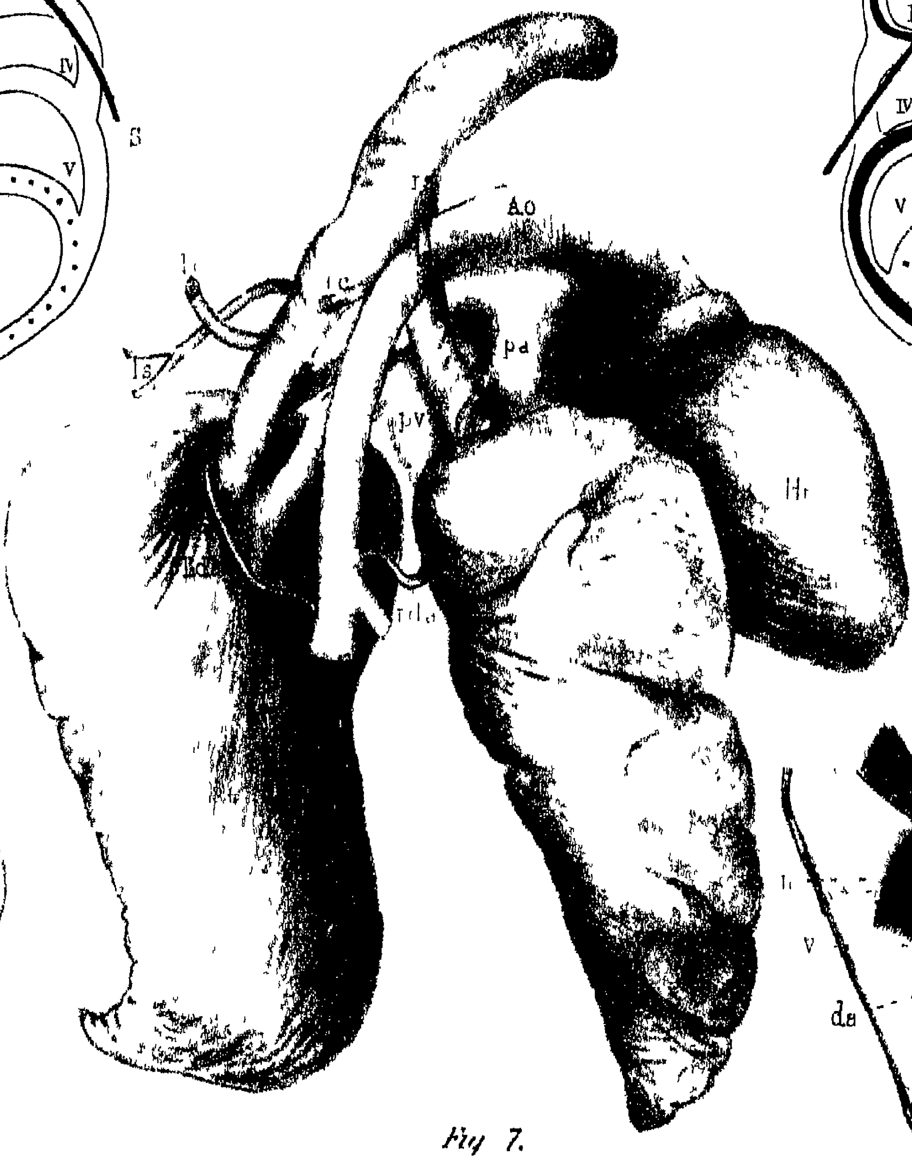


Fig 1



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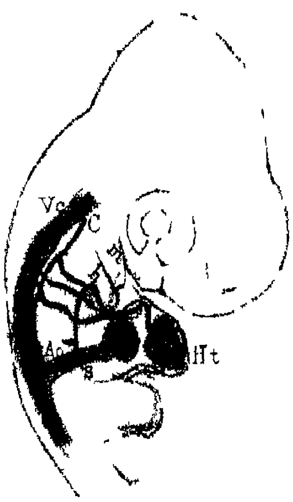

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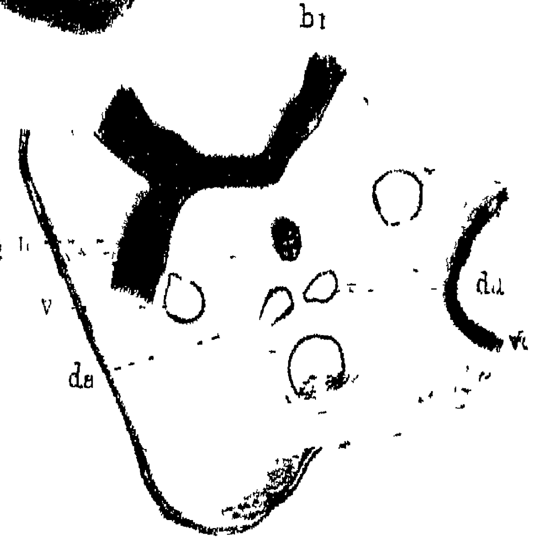
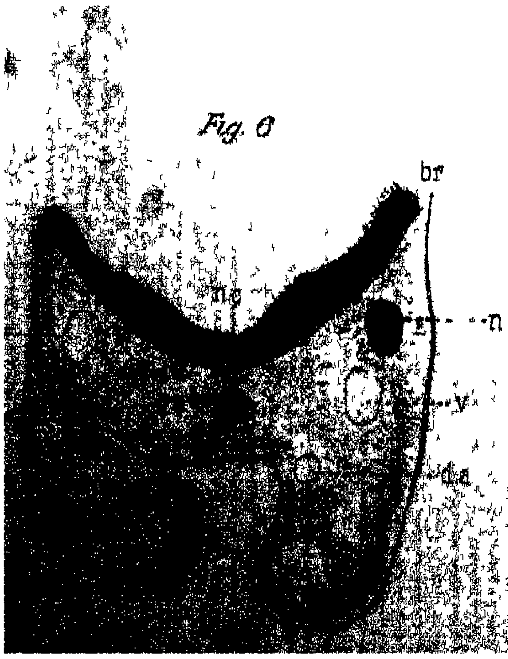
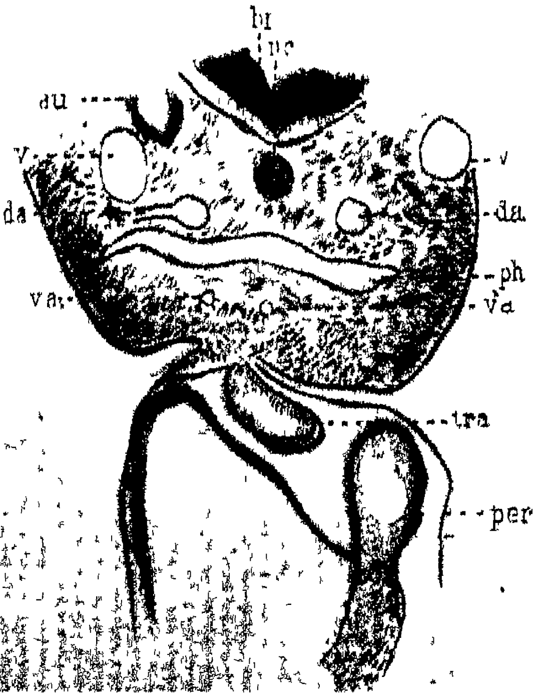


Fig 7.

Fig. 6





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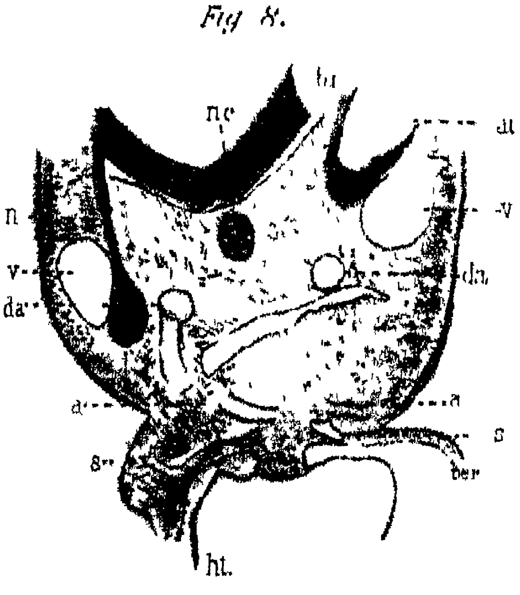

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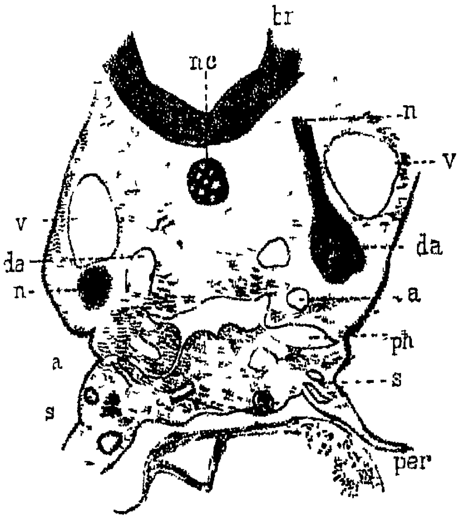

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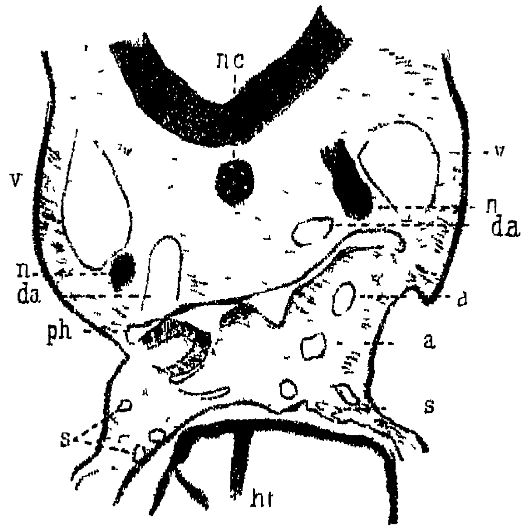

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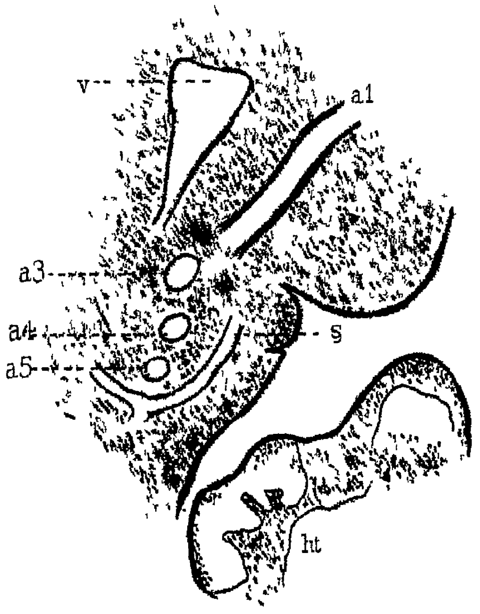

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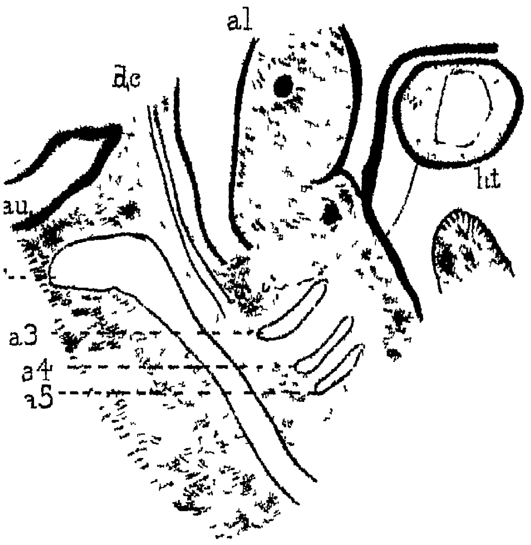

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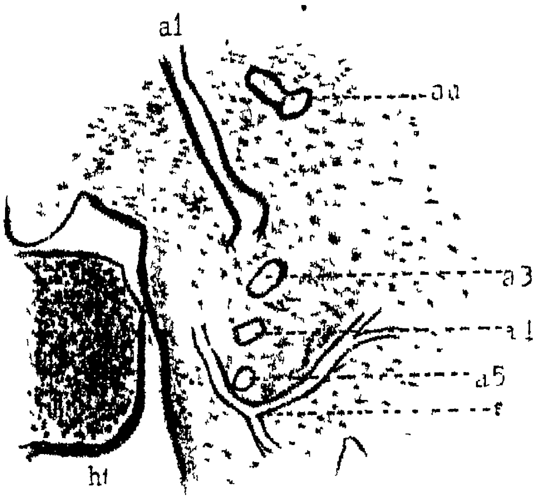

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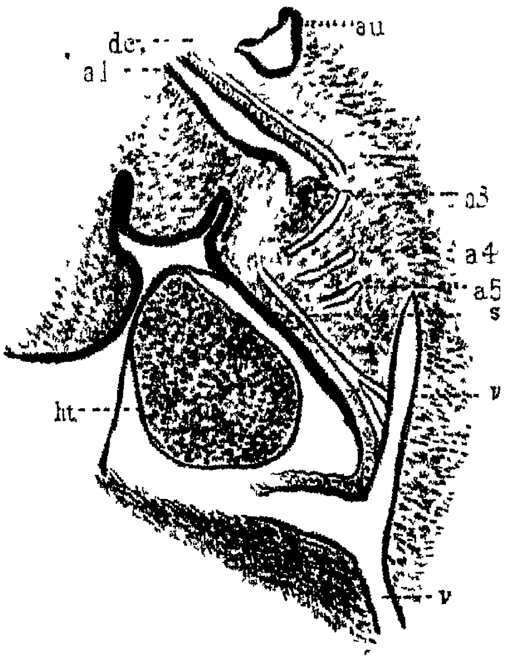
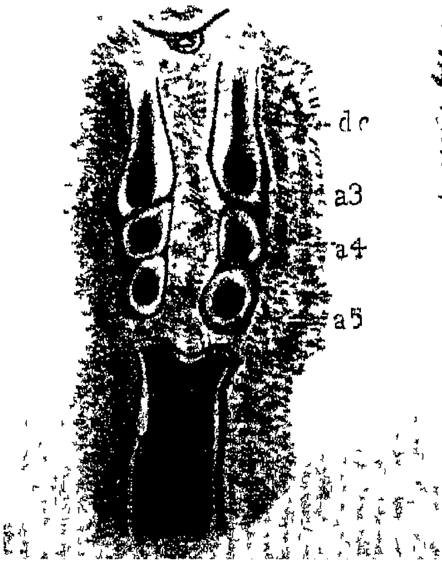


Fig 15



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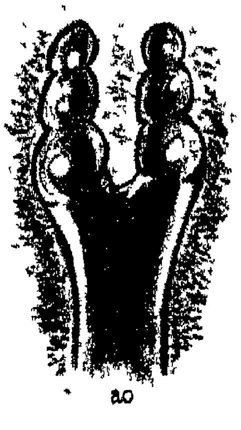

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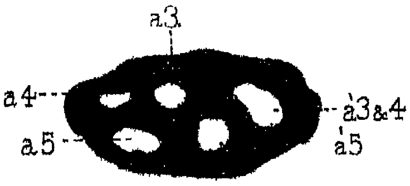

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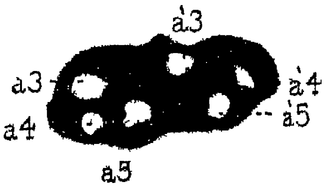

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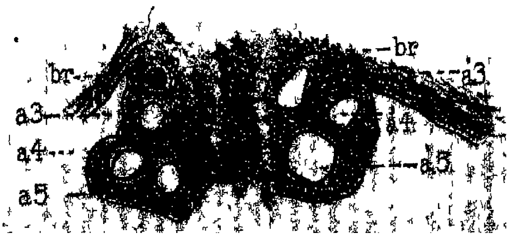

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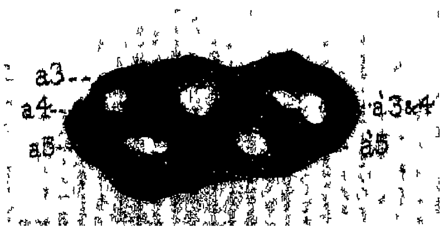

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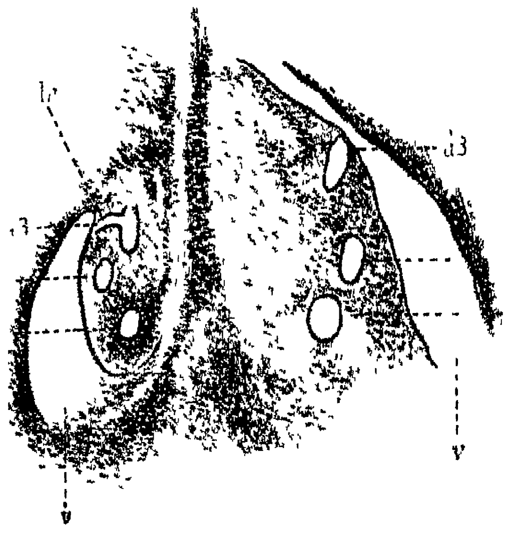

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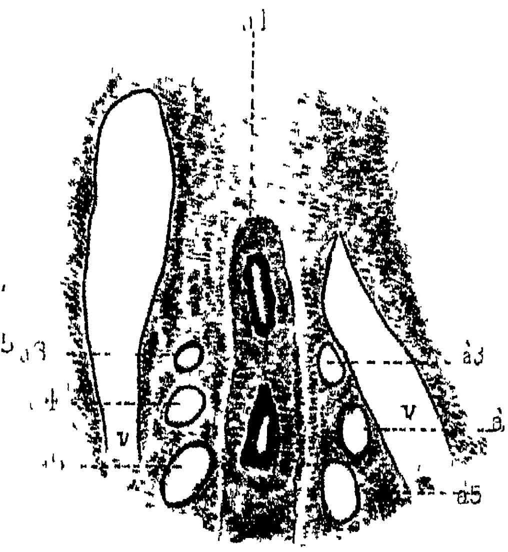

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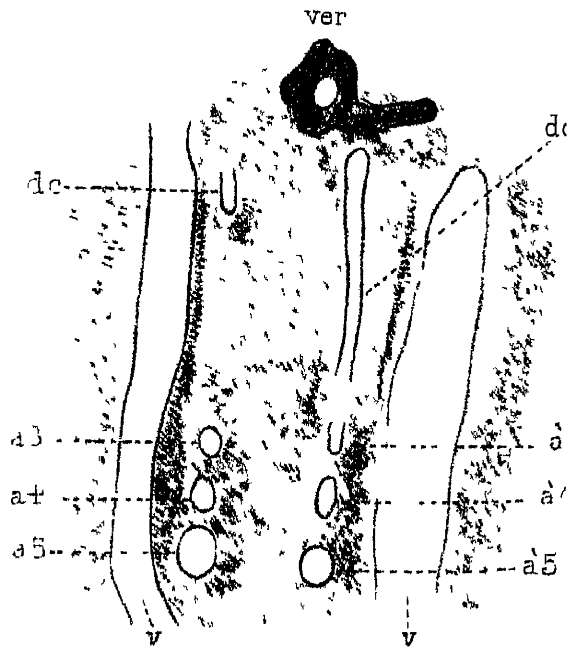

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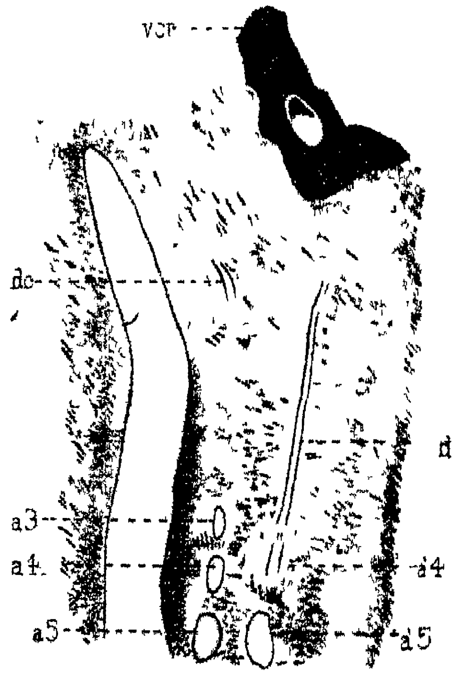

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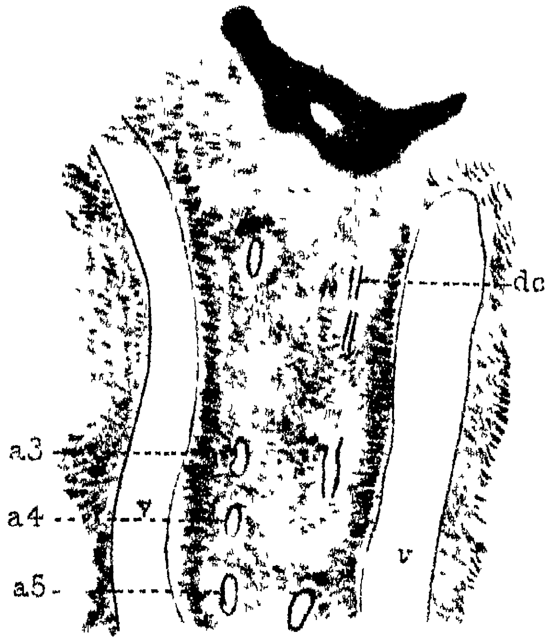

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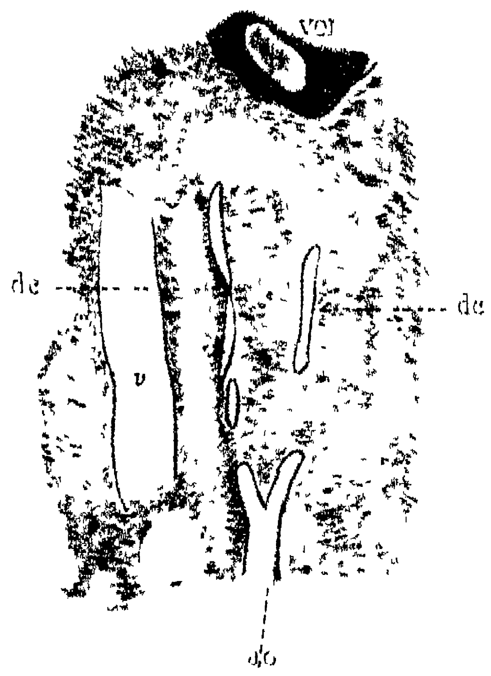

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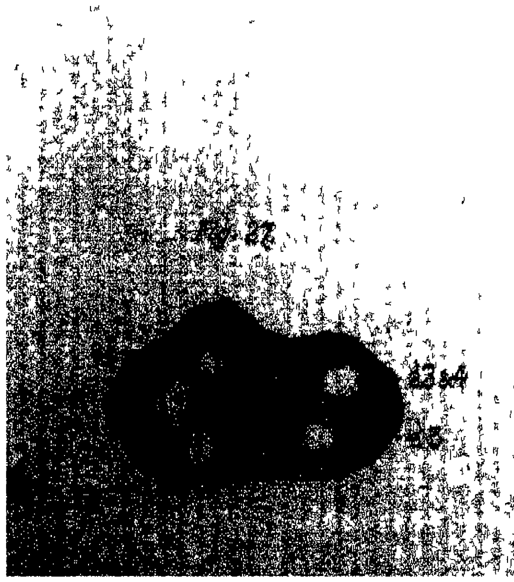

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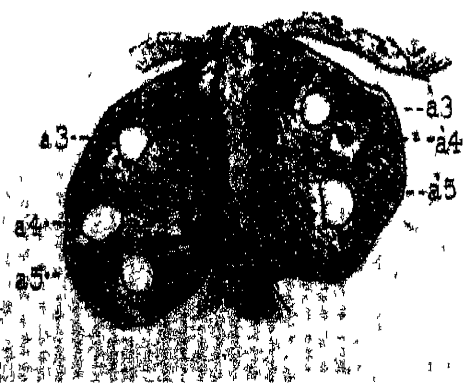

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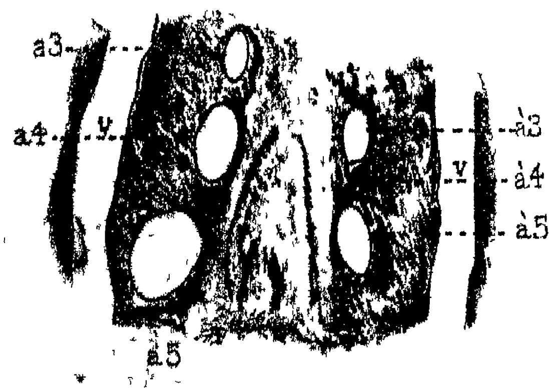

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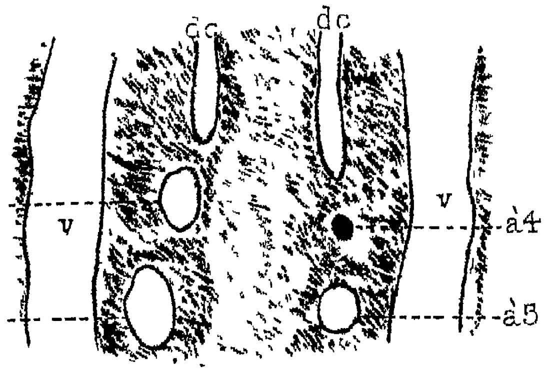

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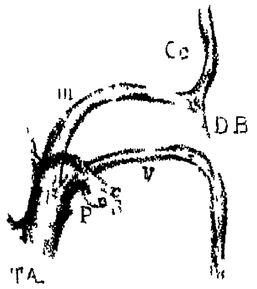

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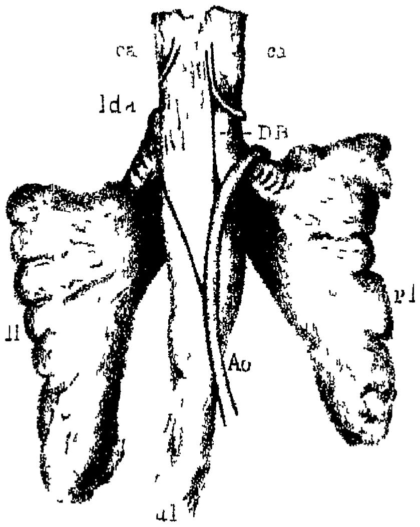

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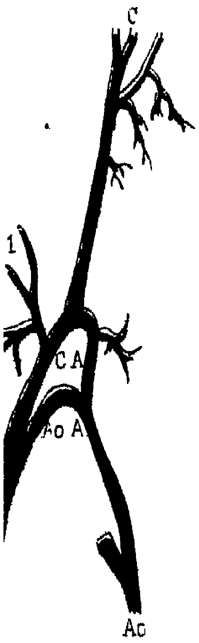

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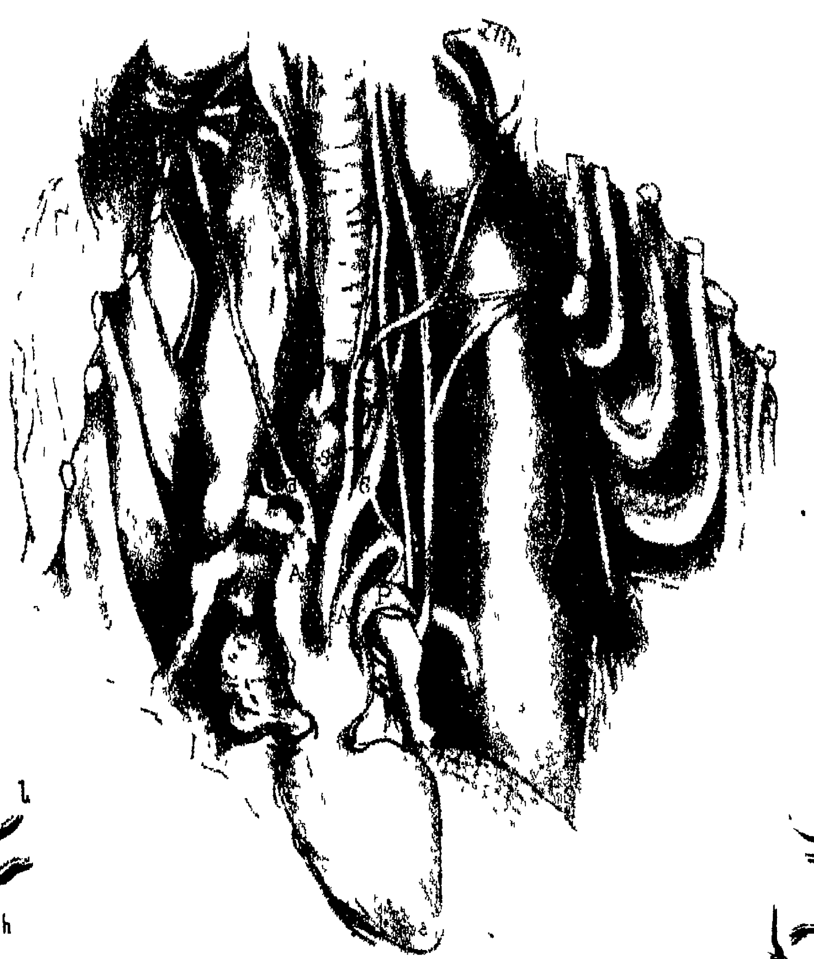

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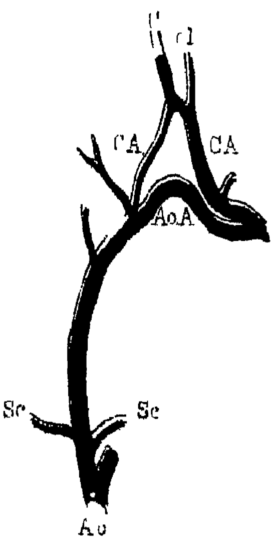

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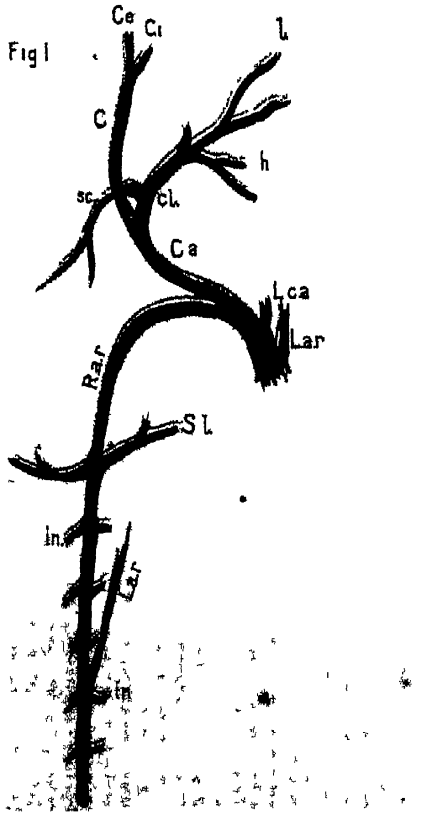

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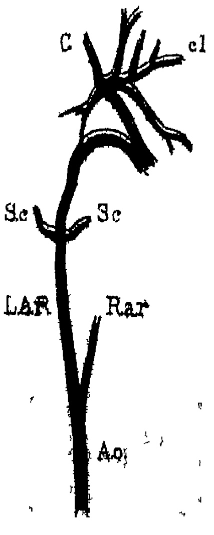

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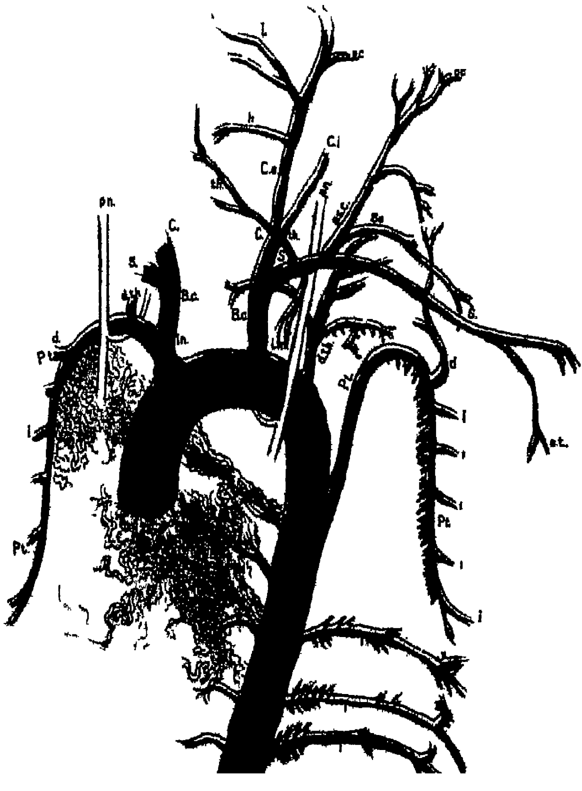
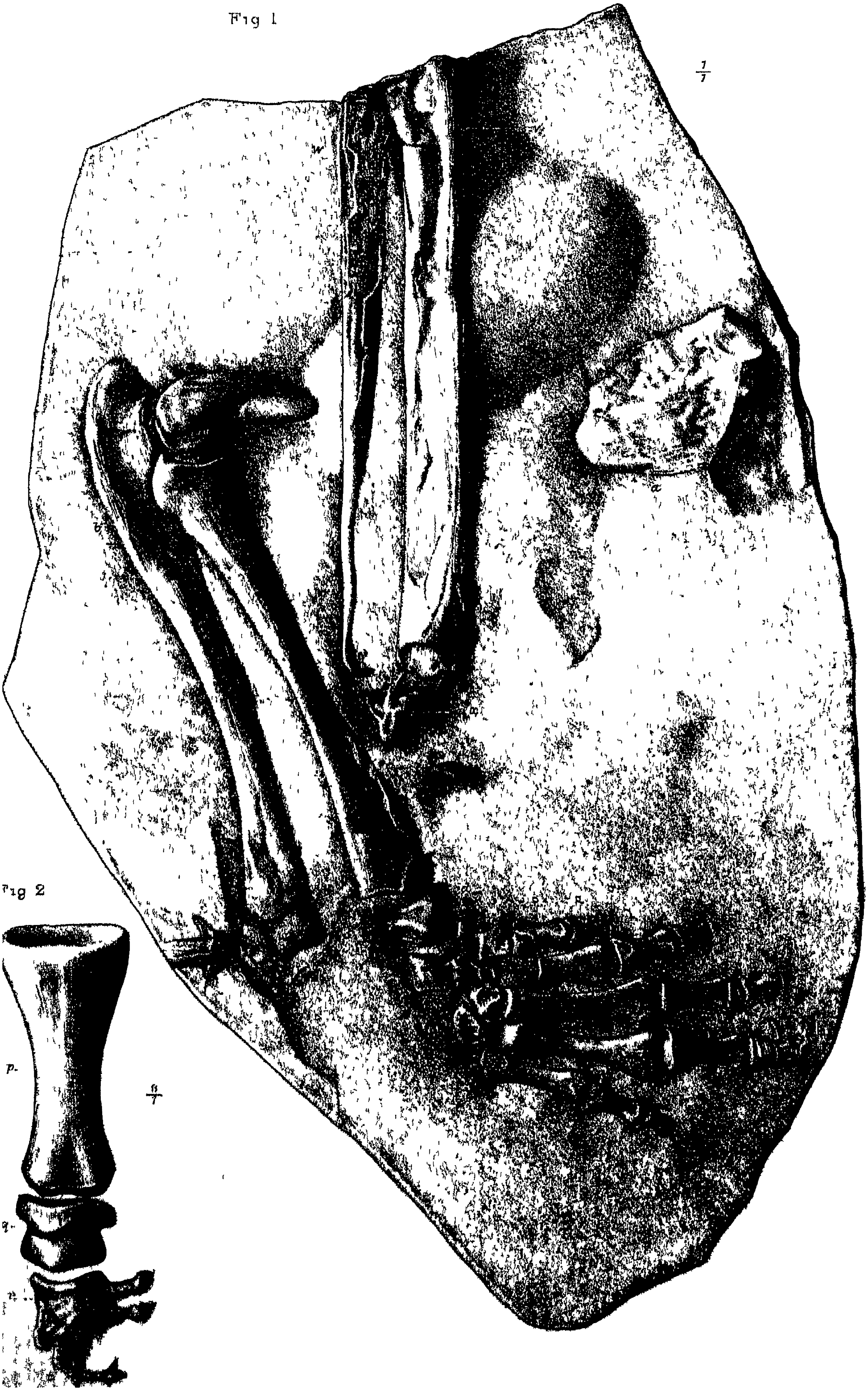


Fig 1



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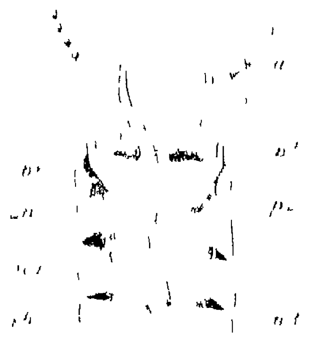

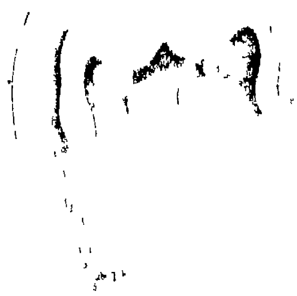

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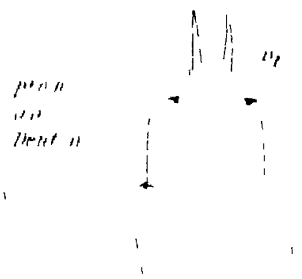

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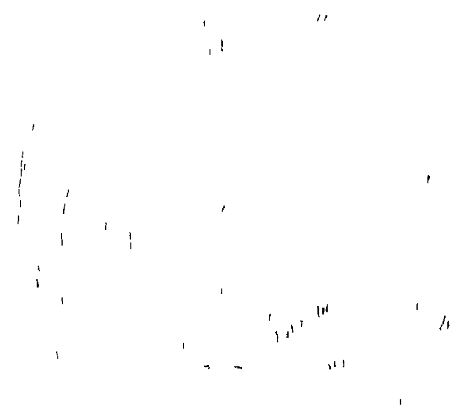

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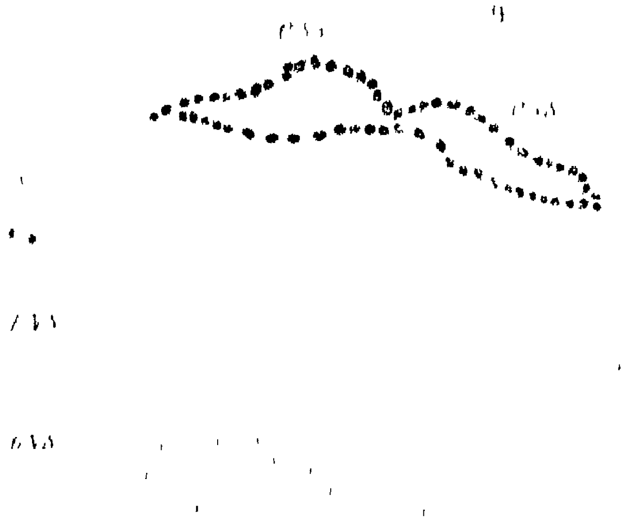

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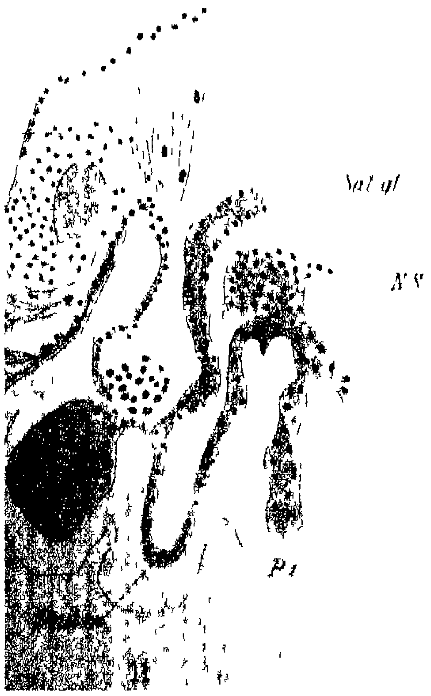

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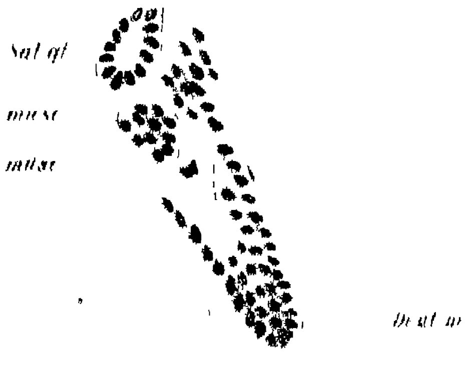

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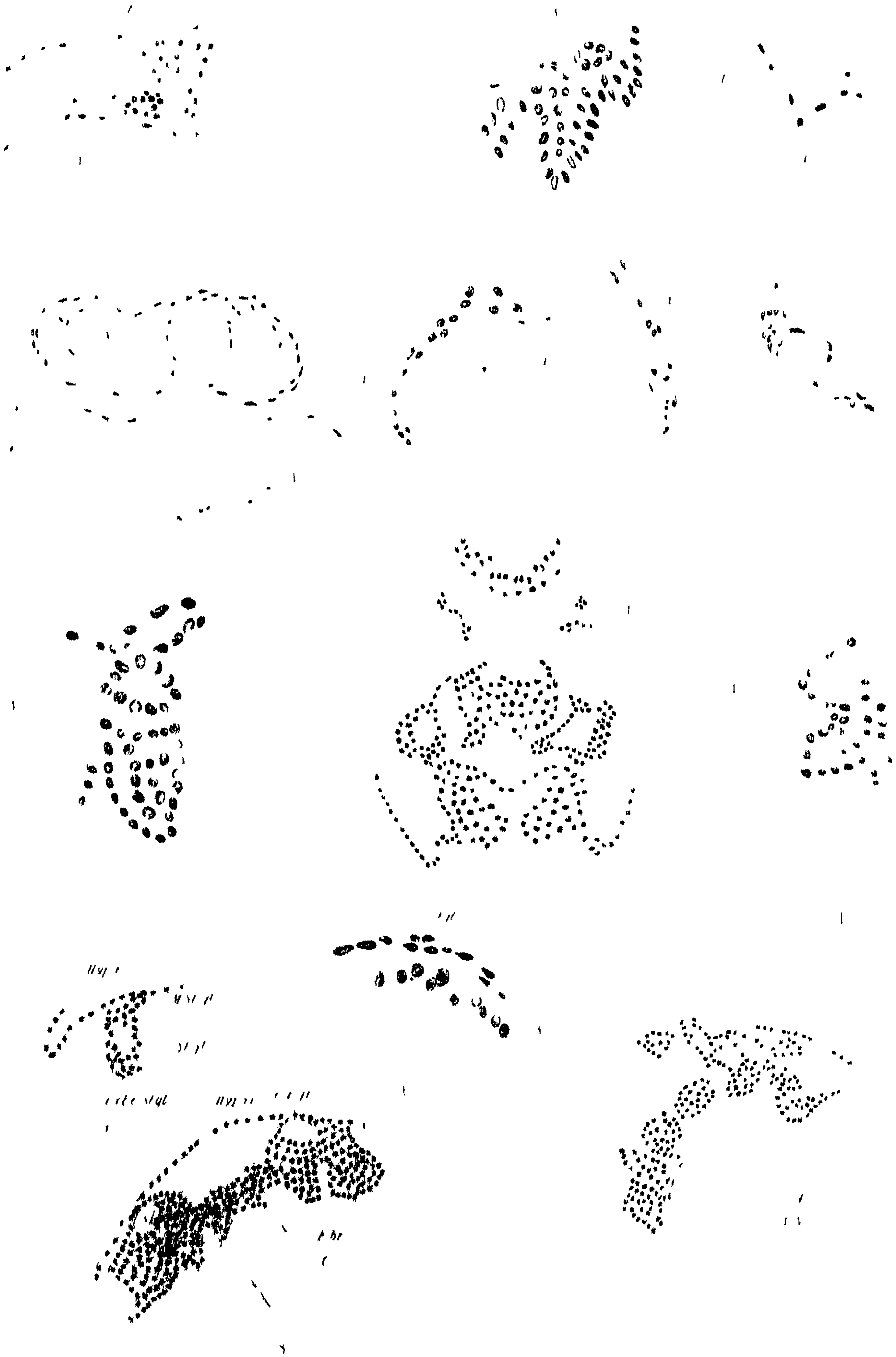

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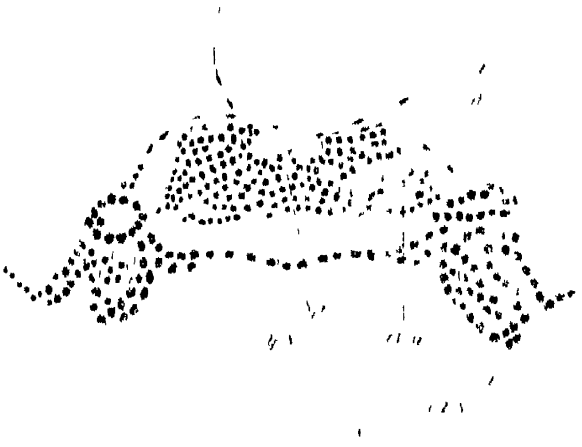

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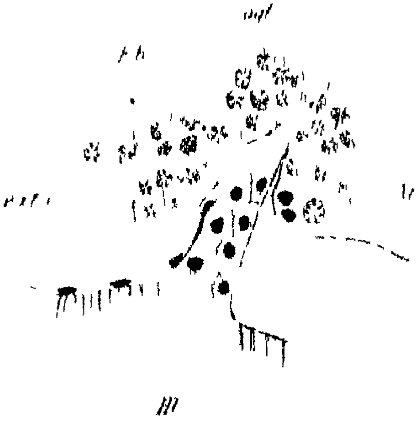
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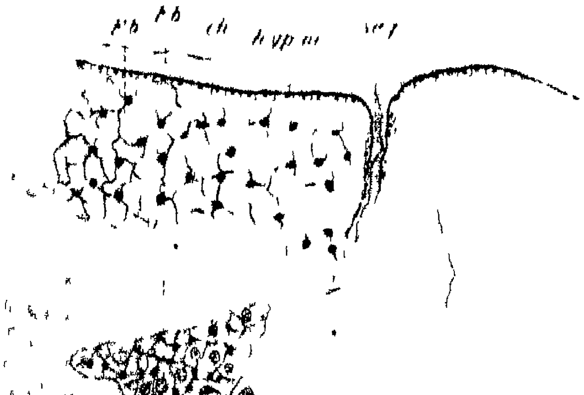
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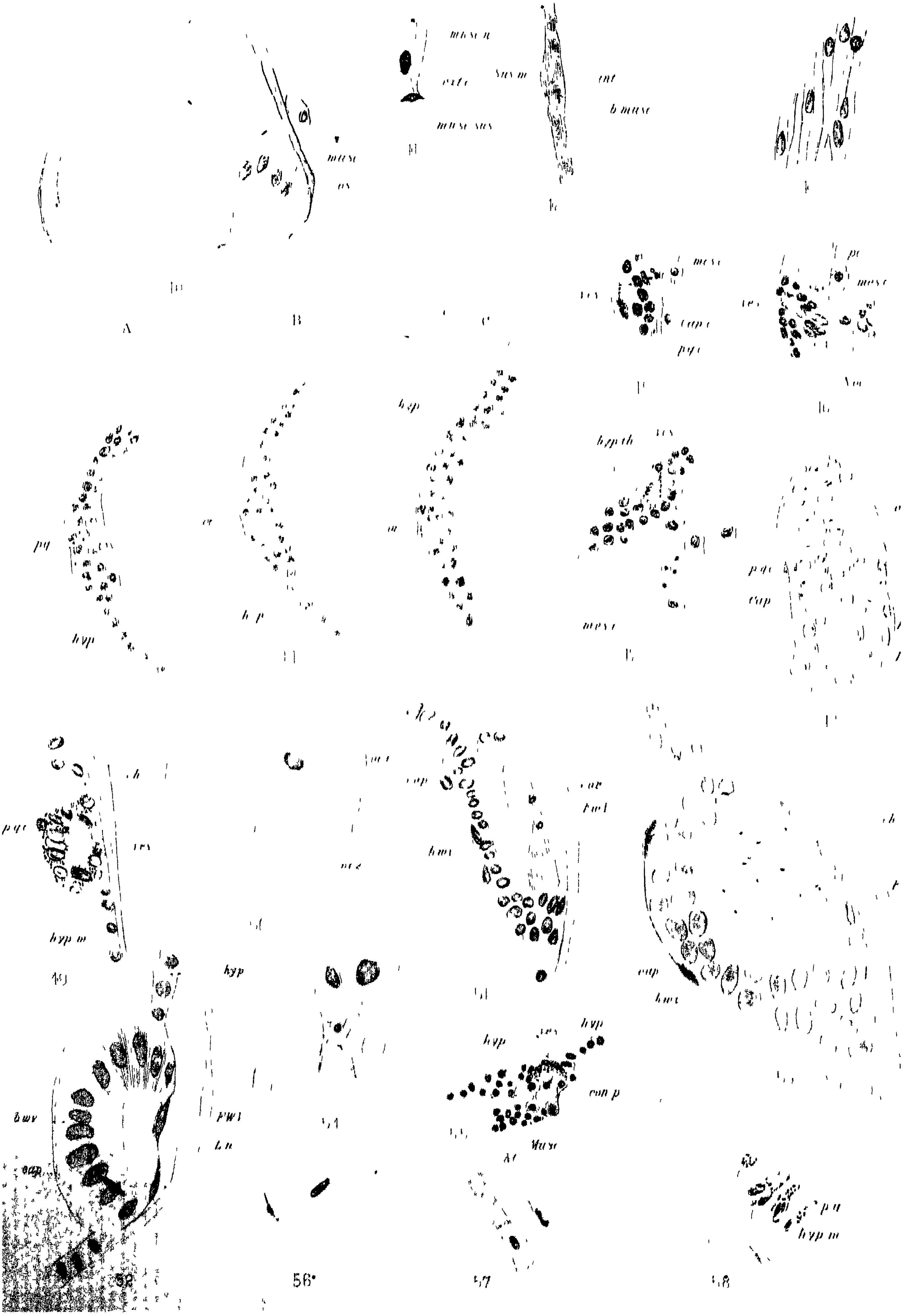
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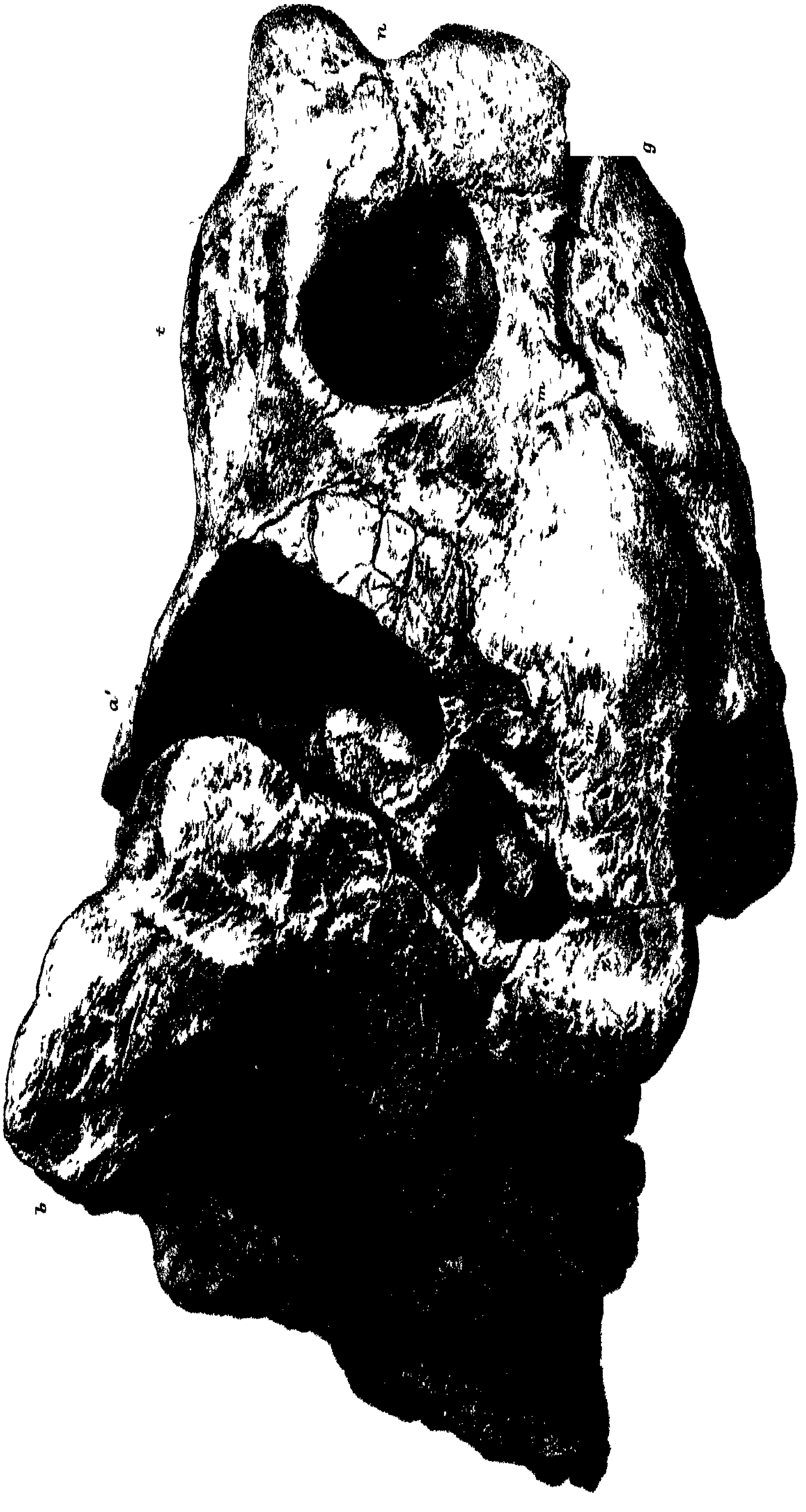
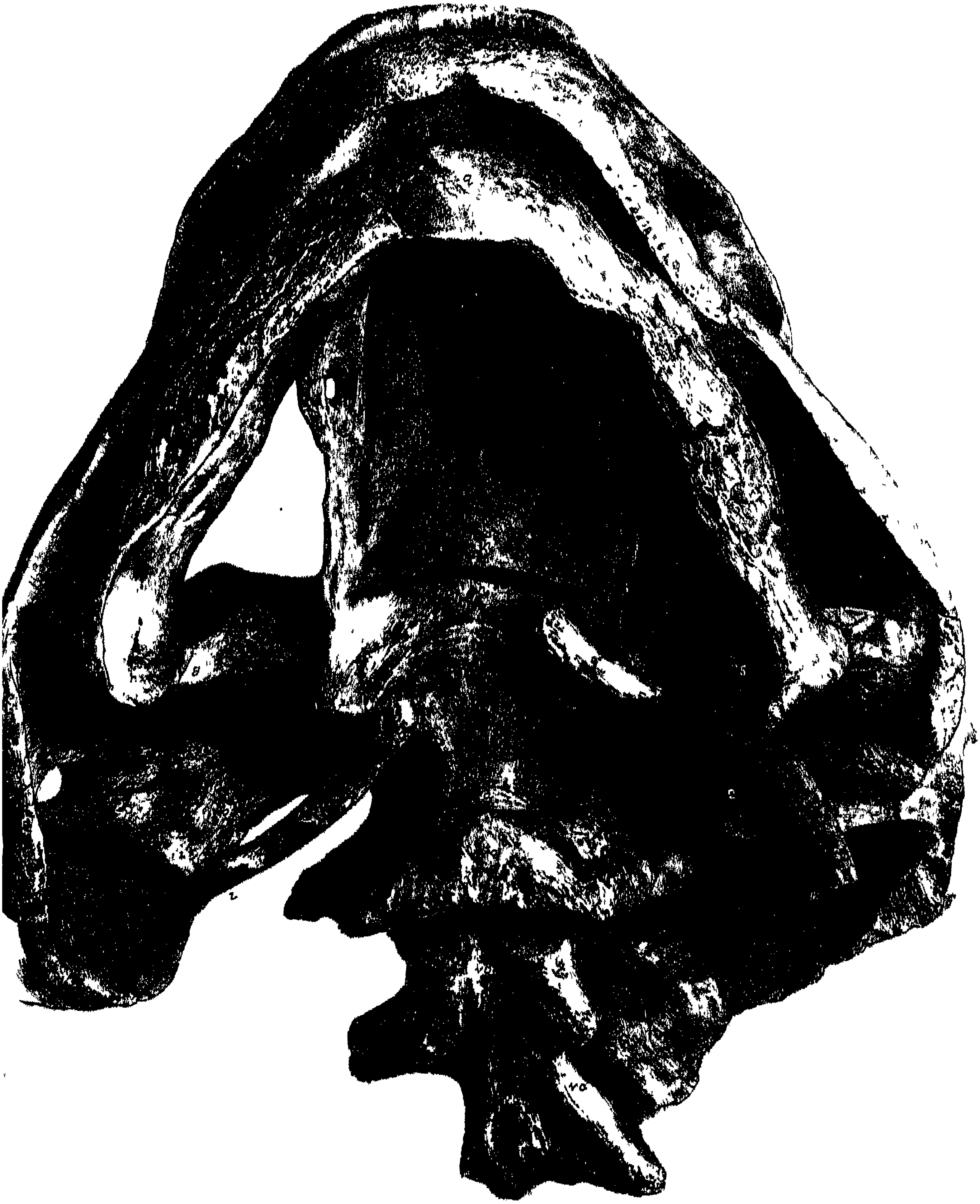


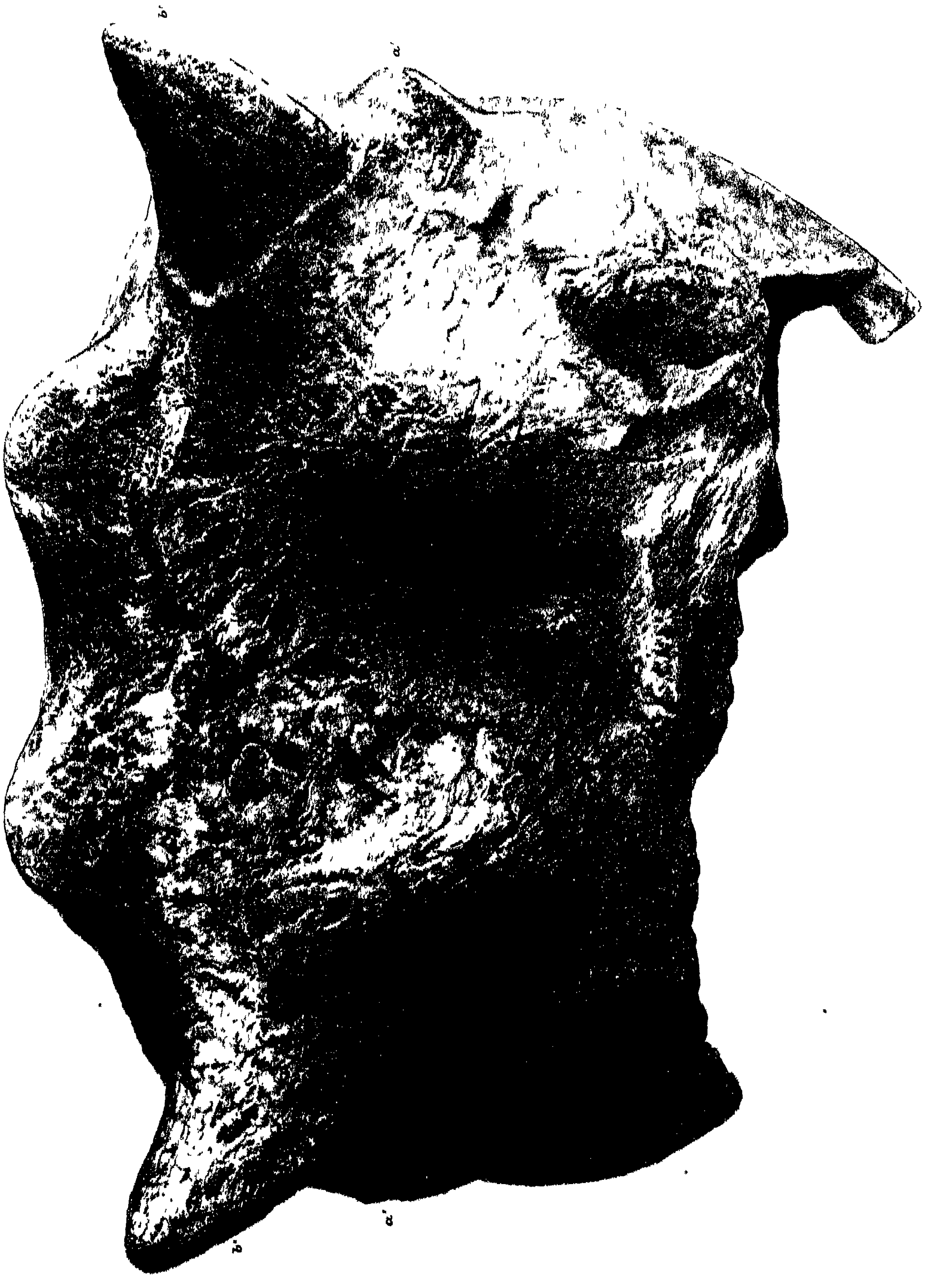
ania platyceps

West Newman & Co imp.

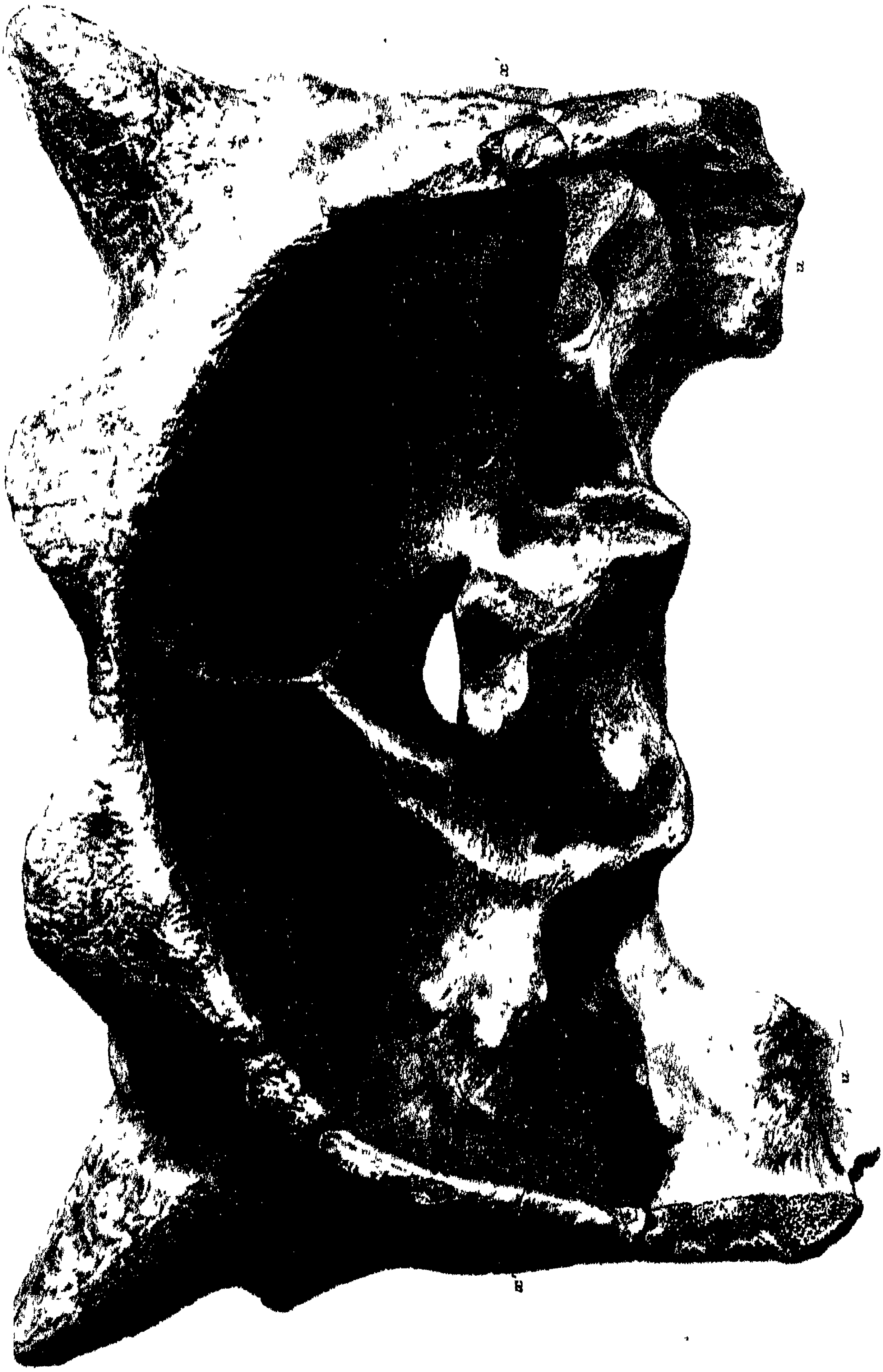


West Newman & Co.

Base view of skull of Meiolania platyceps

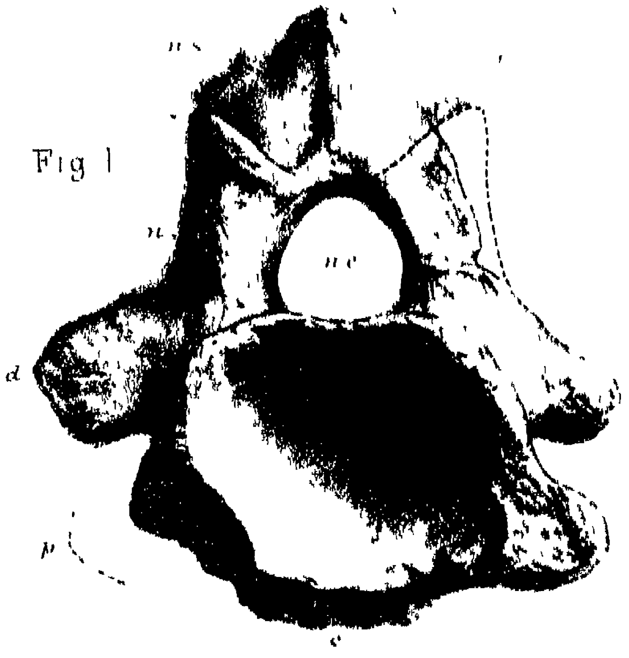


UPPER SURFACE OF HINDER PORTION OF CALVARIUM MEIOLANIA PLATYCEPS



BASE OF THE SKULL OF MEIOLANIA PLATYCEPS

Fig 1



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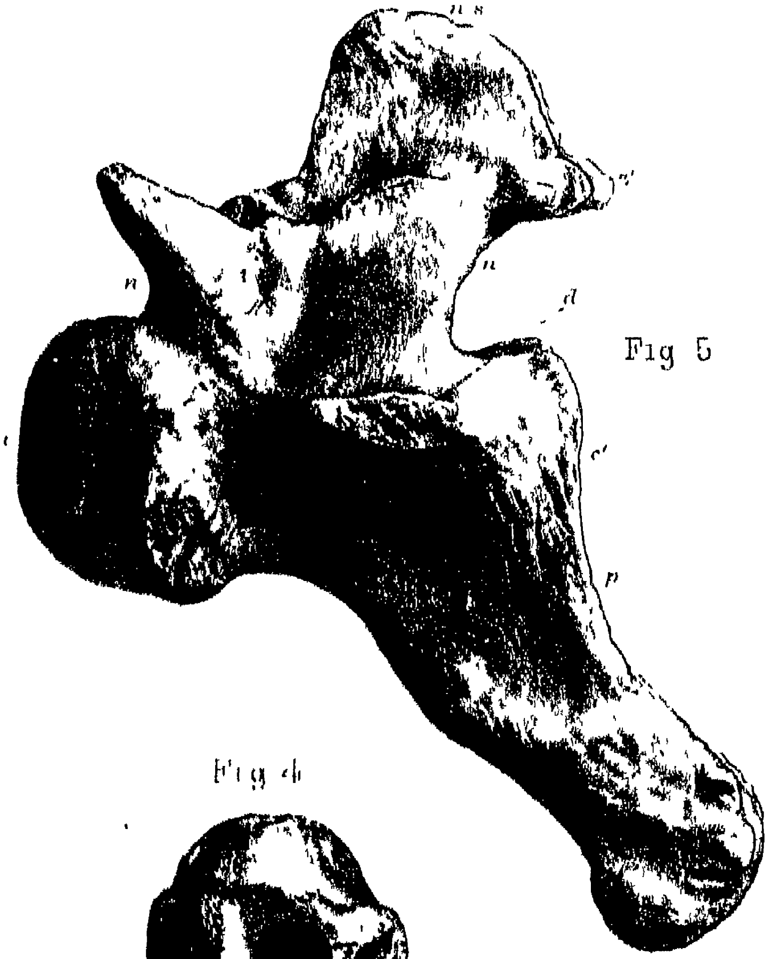

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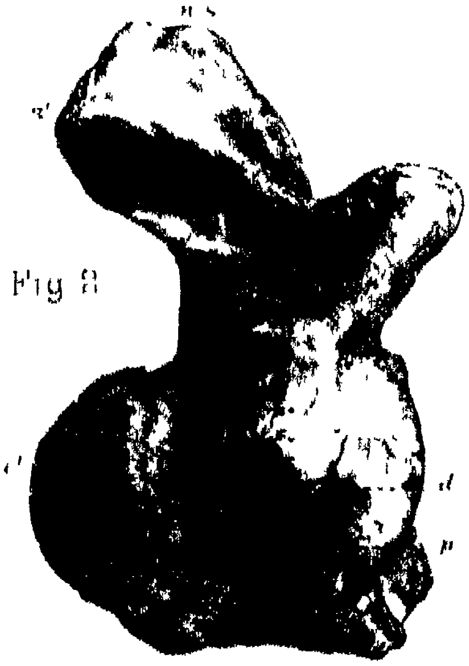


Fig 4

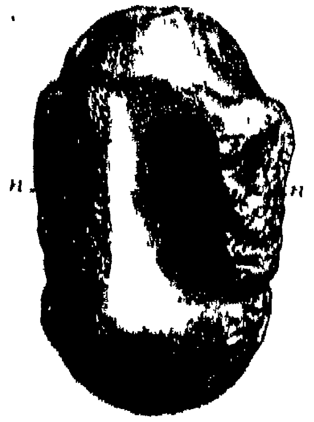
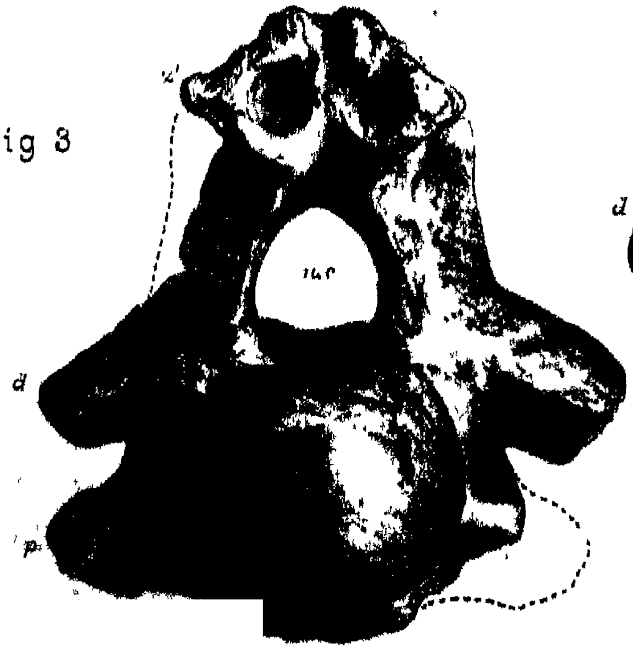


Fig 3



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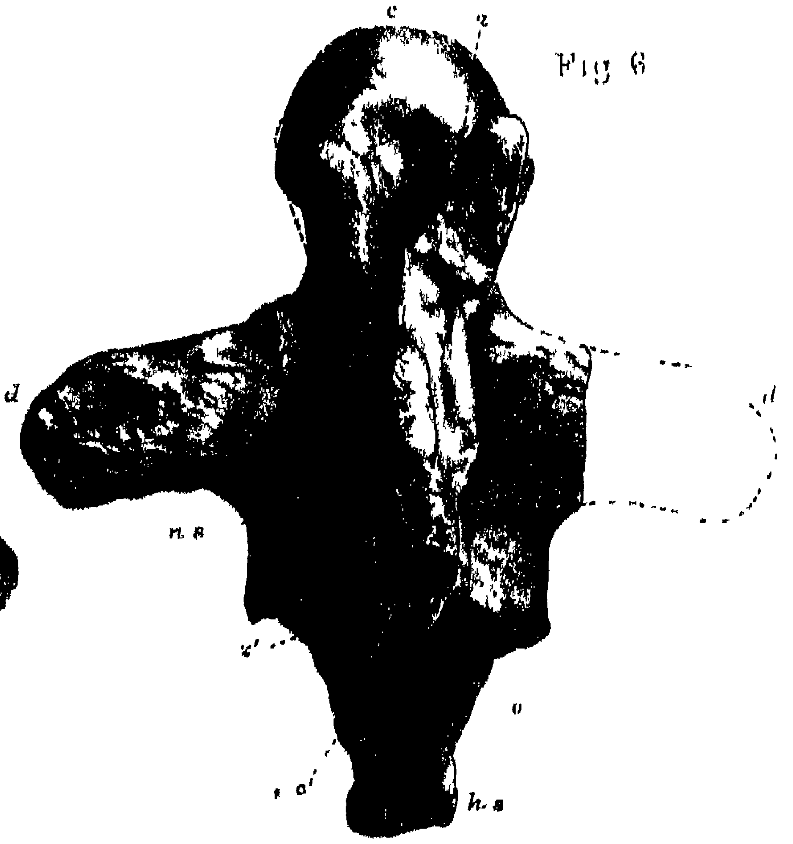


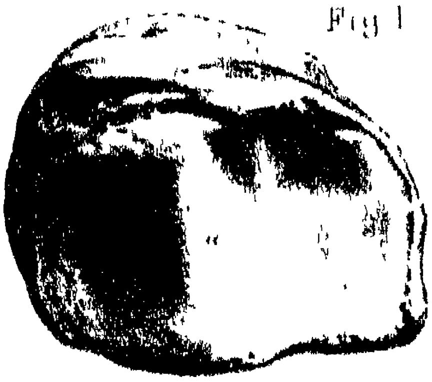


Fig 1

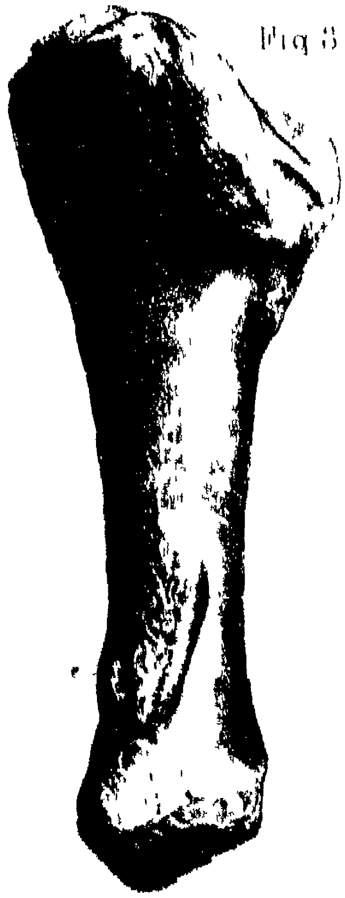
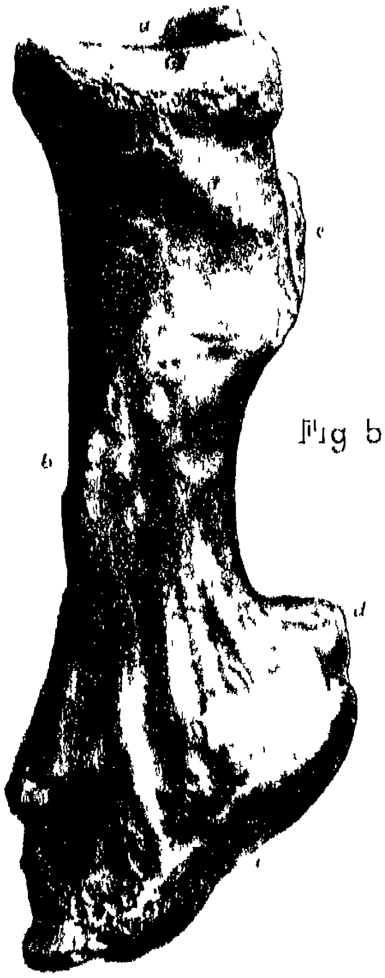


Fig 3



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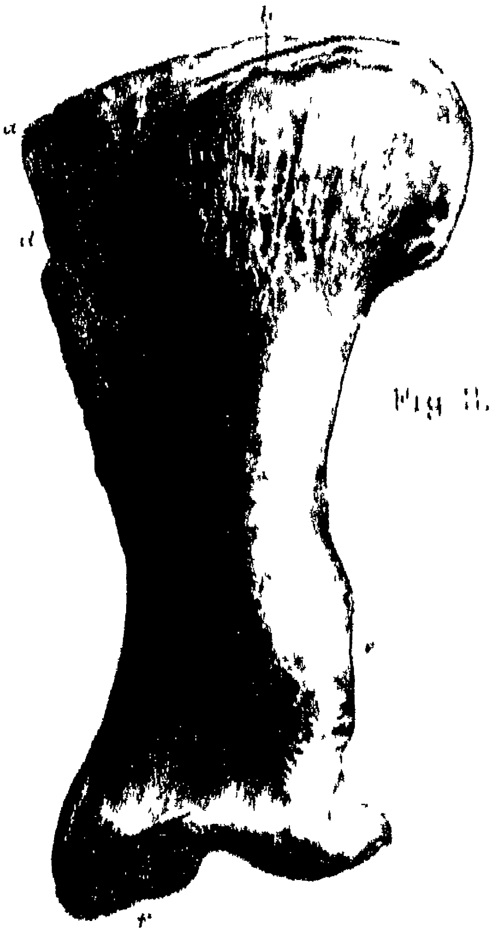

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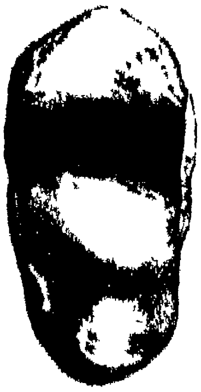

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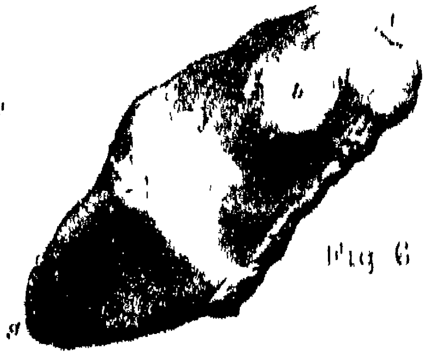
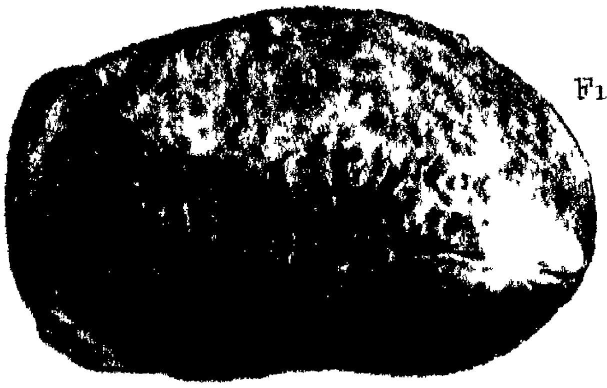


Fig 6

Fig 7



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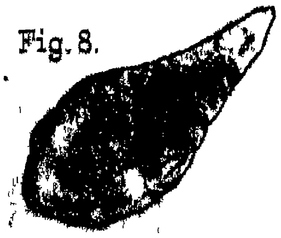

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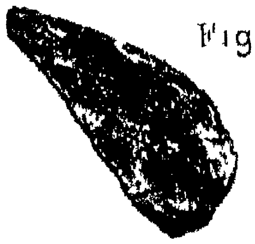

Fig 9

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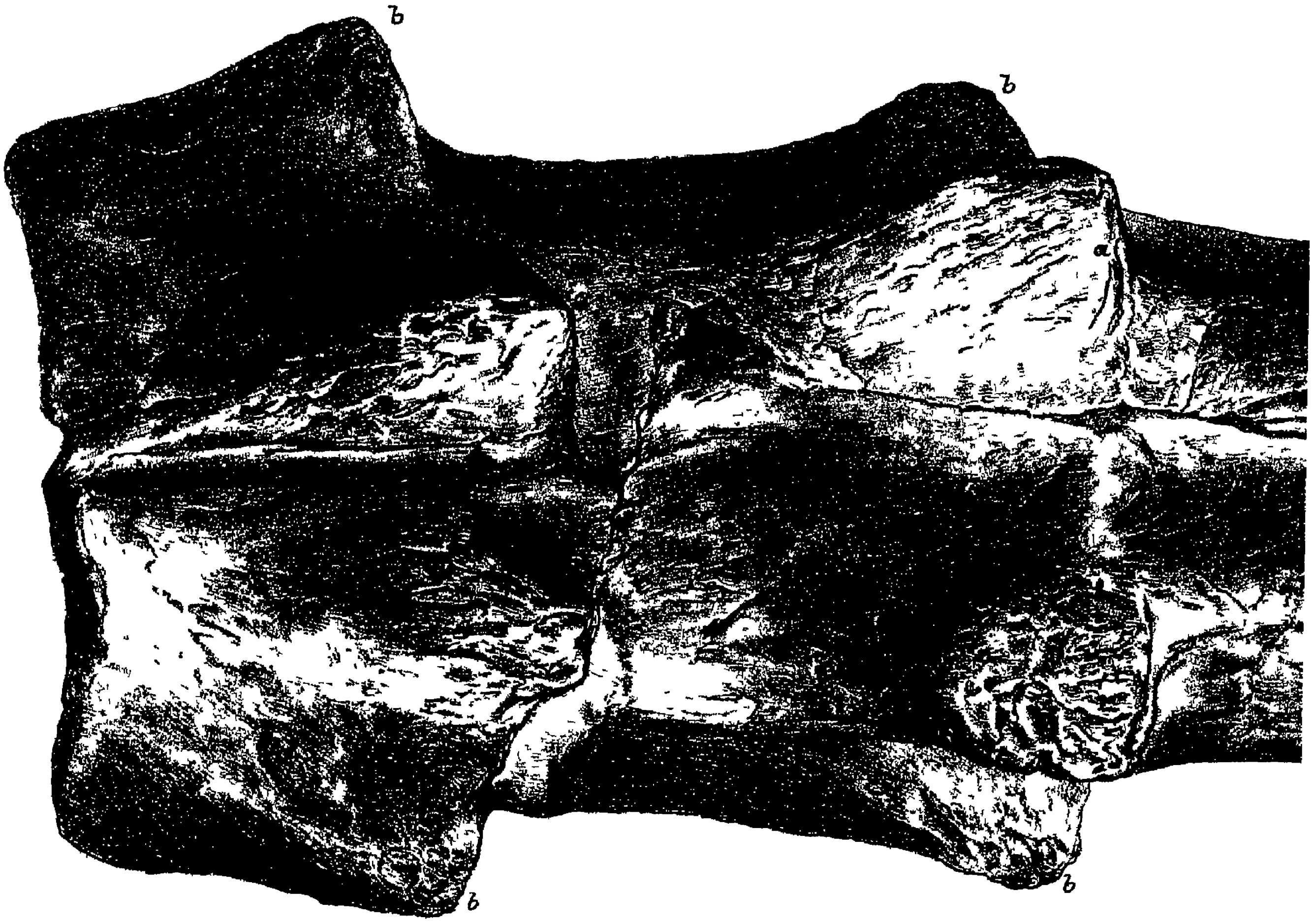


Coalesced terminal segments o

Meiolania plat

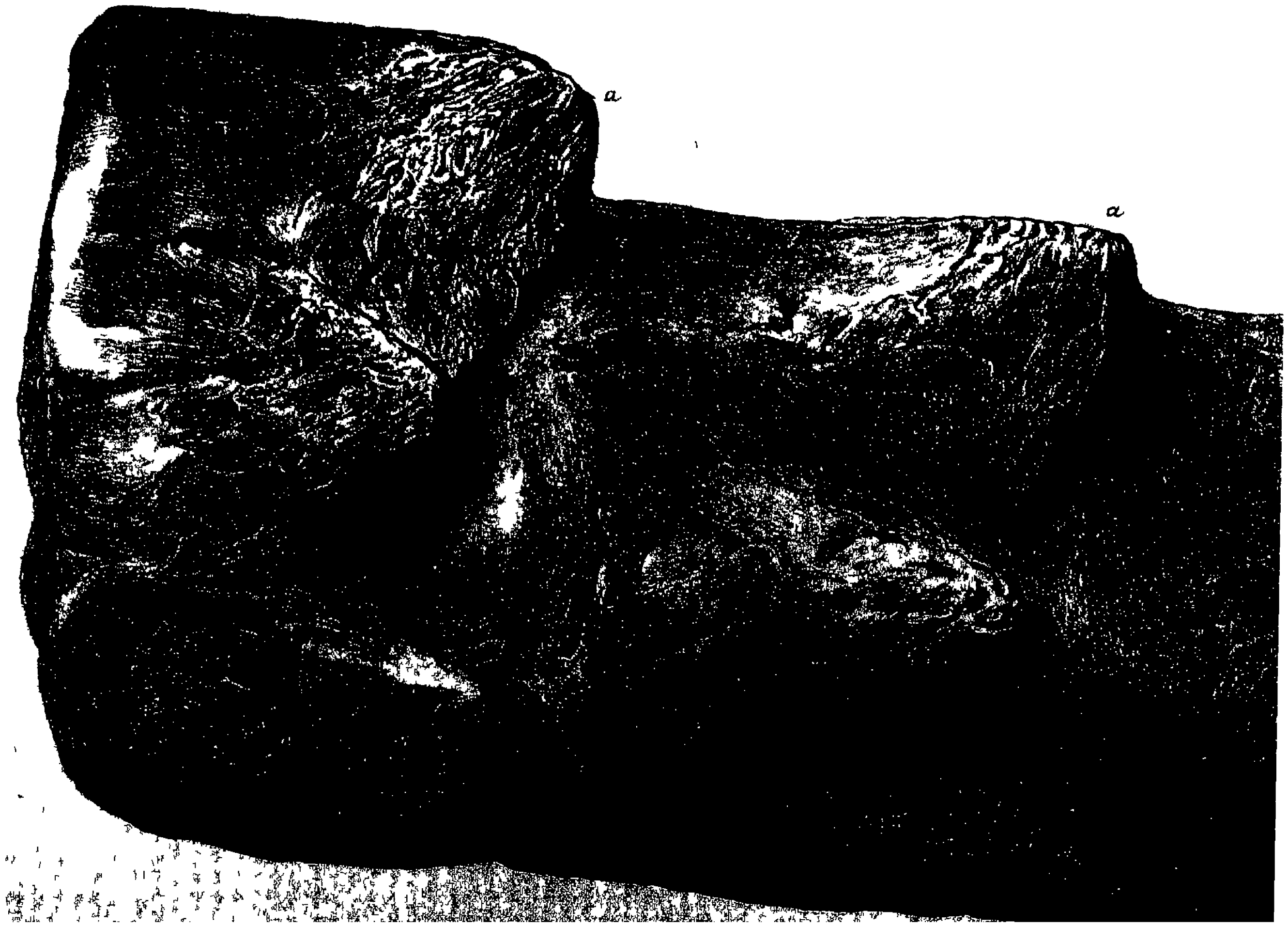
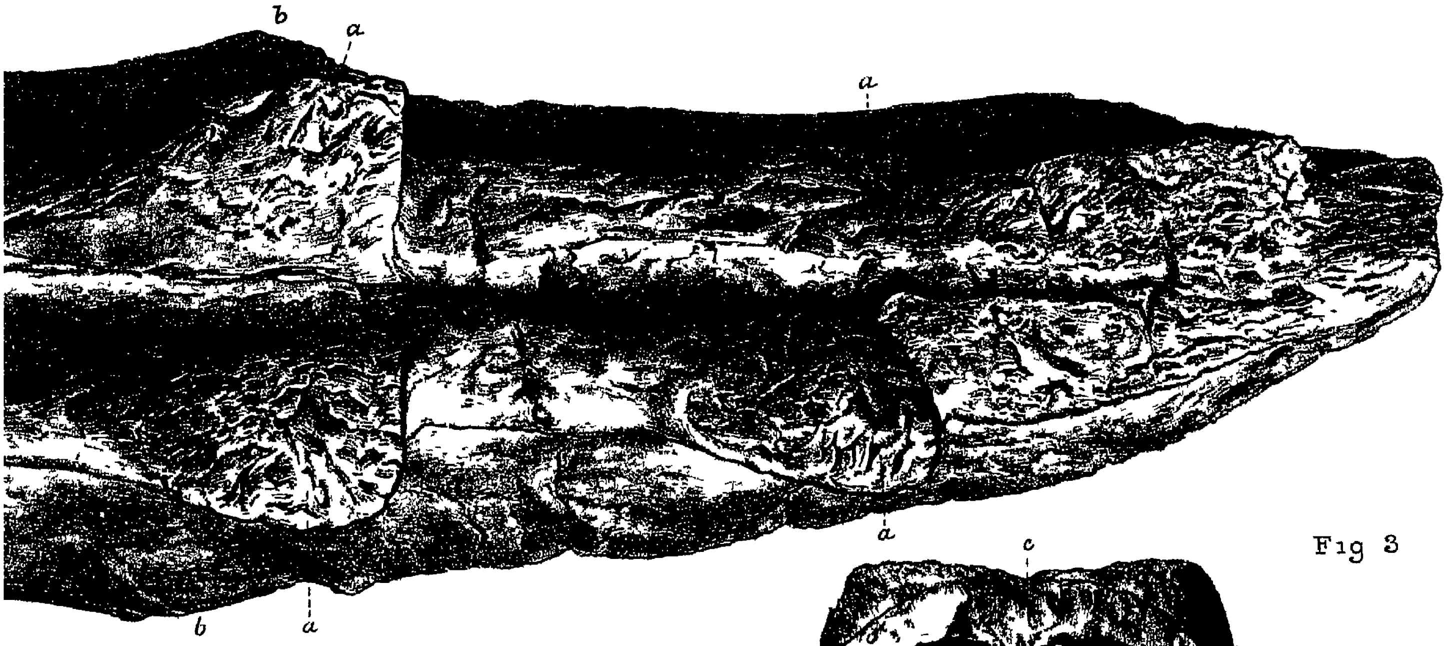


Fig 1



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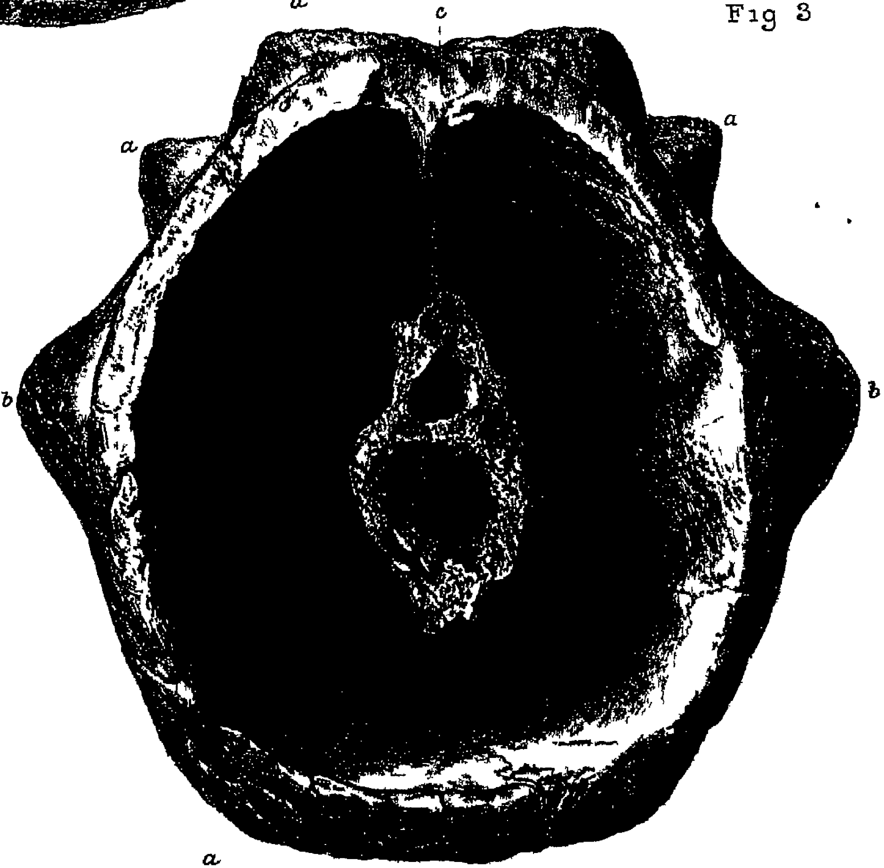

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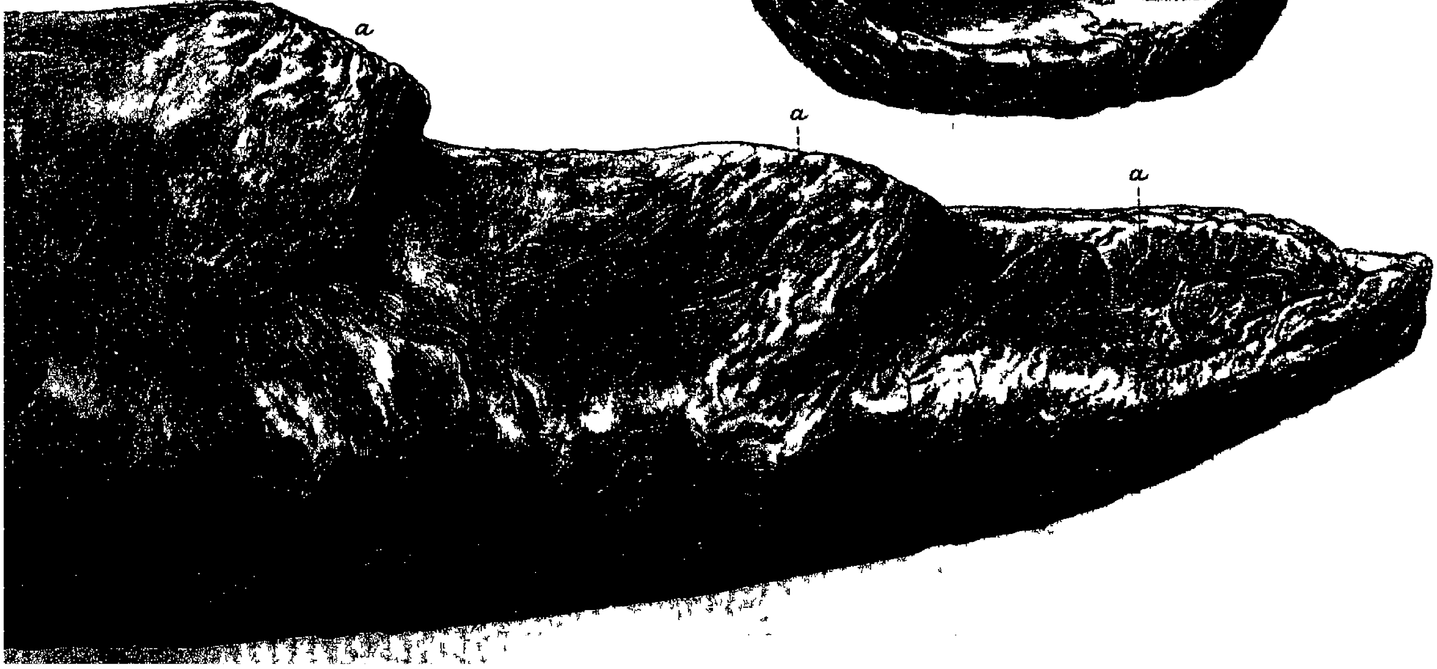
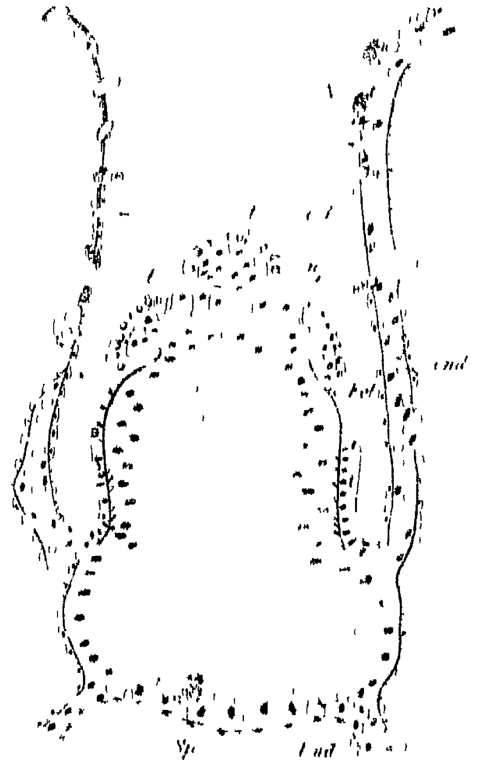
Fig 2

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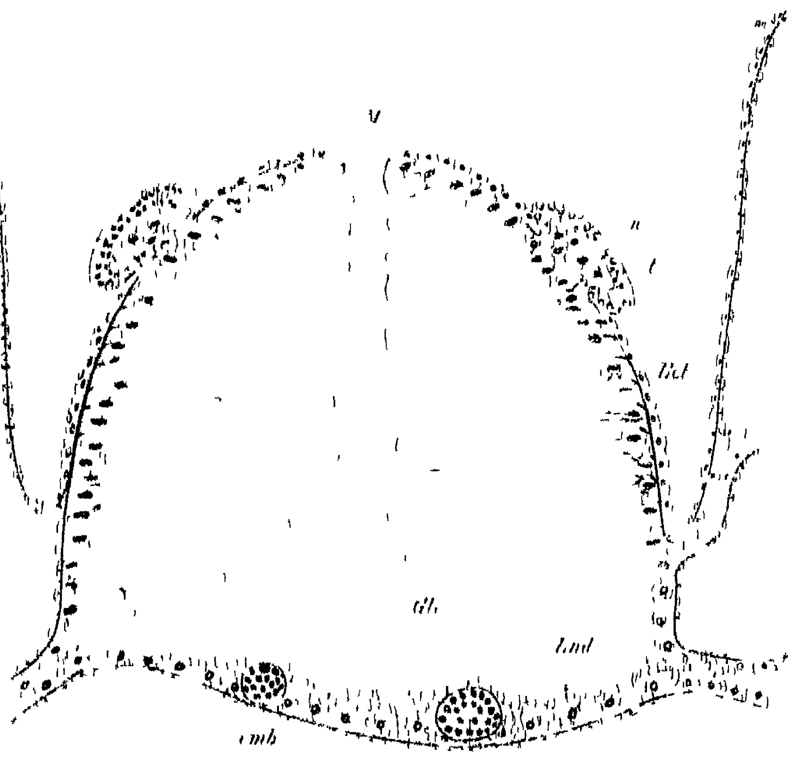
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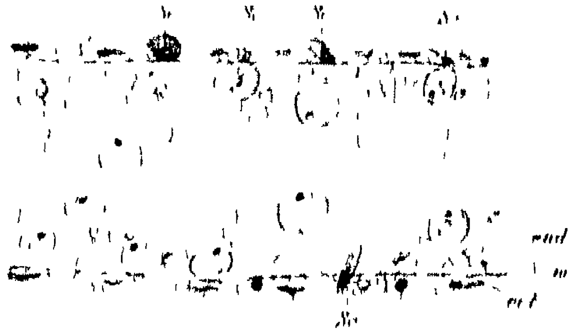
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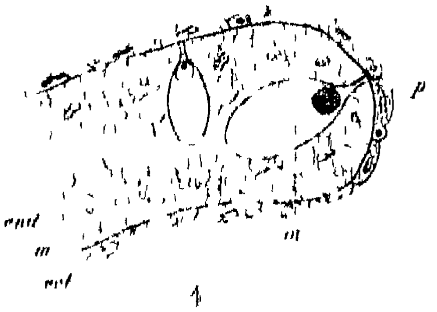
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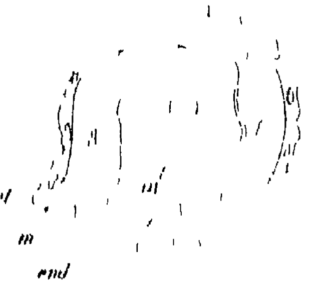
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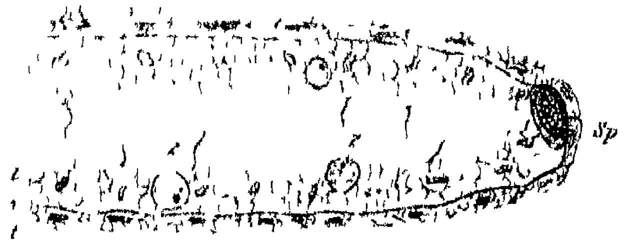
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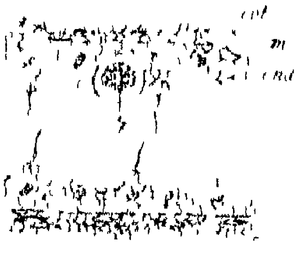
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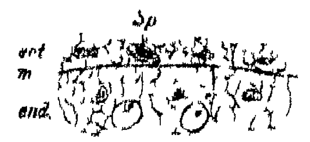
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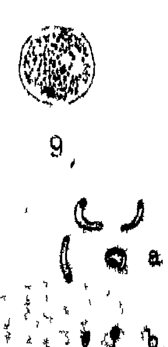
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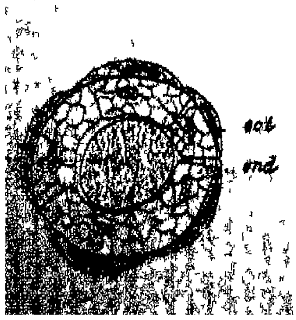
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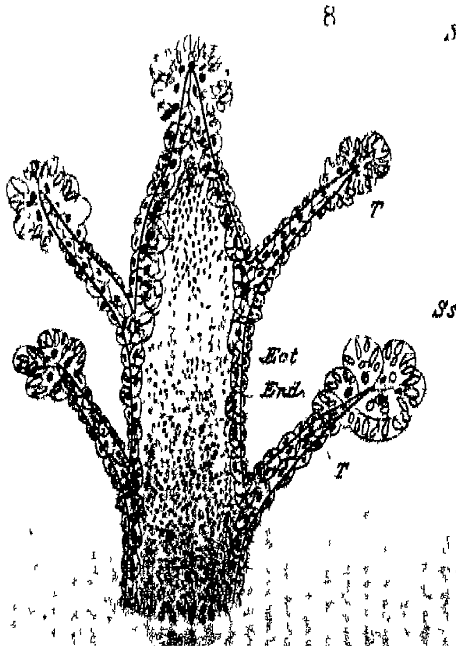
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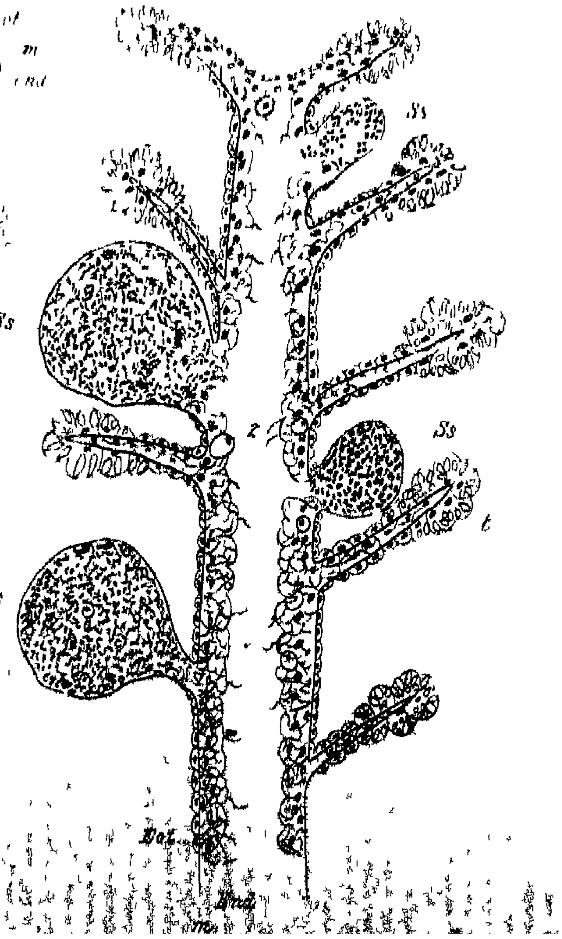
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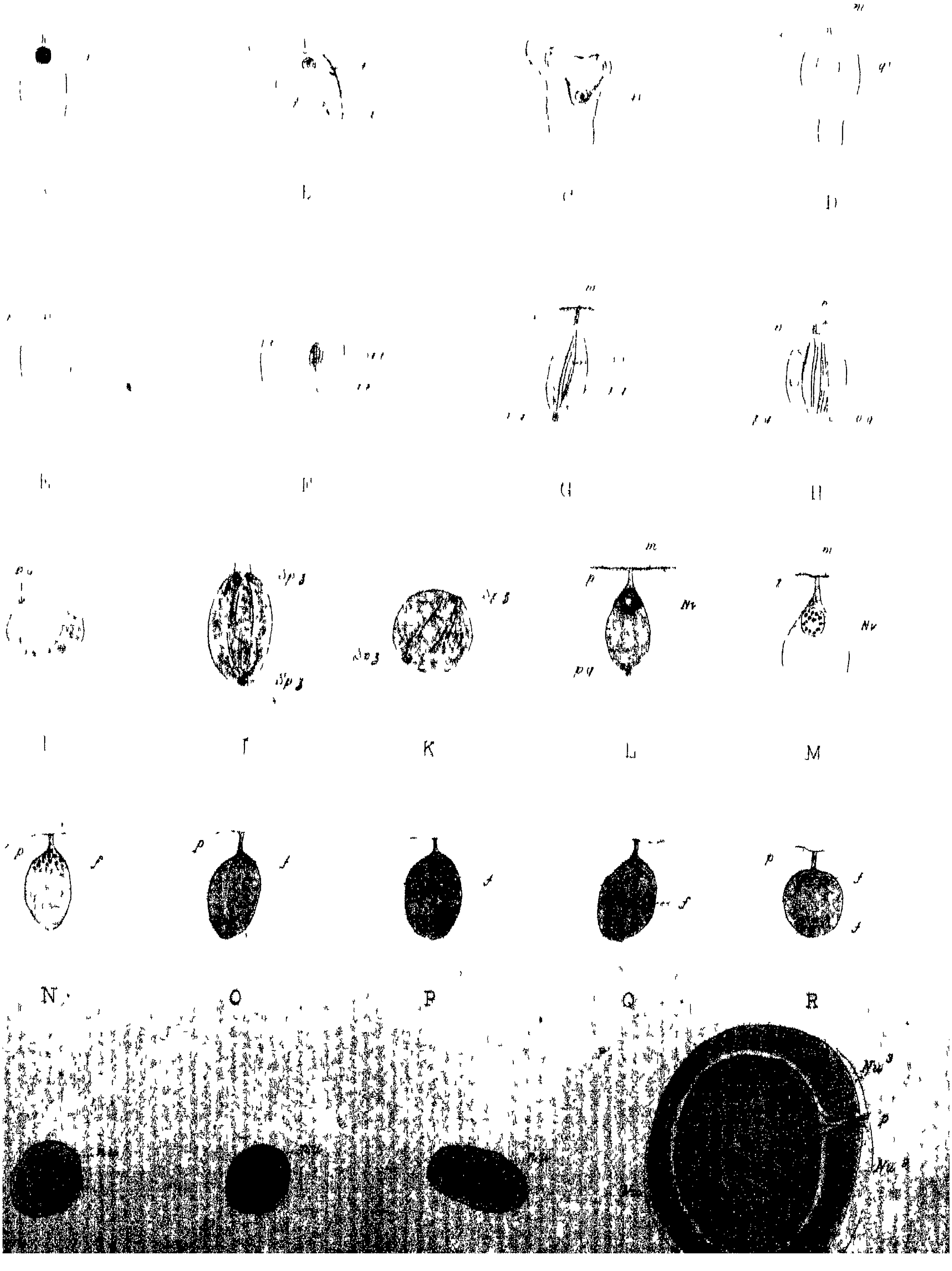
Fig 14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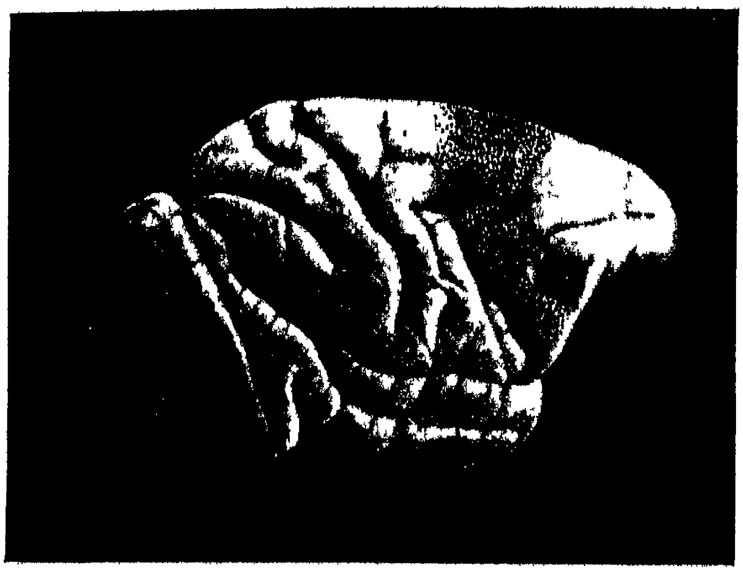


Fig. 4.—ABSOLUTE REPRESENTATION OF TURNING OF THE HEAD TOWARDS THE OPPOSITE SIDE.

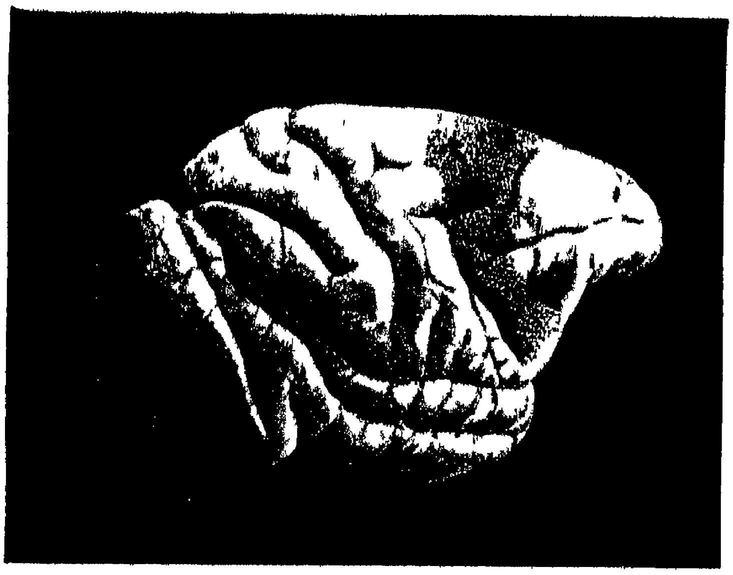


Fig. 4*a*.—PRIMARY REPRESENTATION OF TURNING OF THE HEAD TOWARDS THE OPPOSITE SIDE

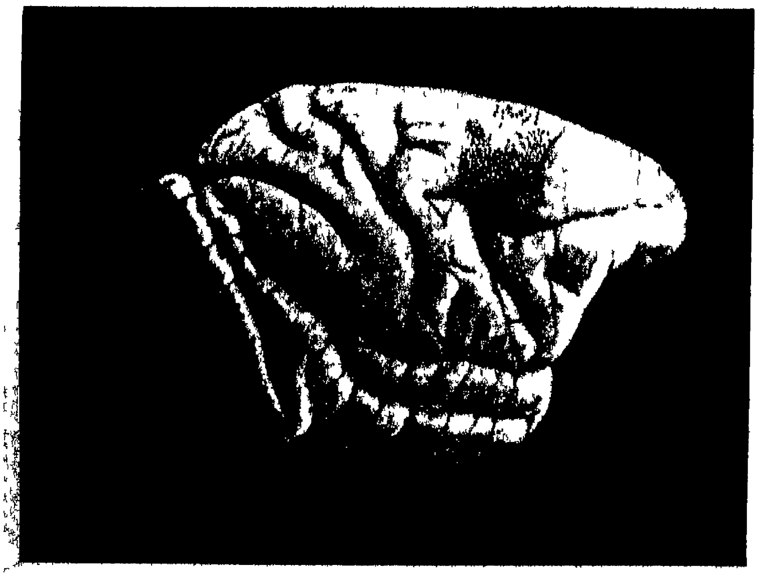


Fig. 5.—PRIMARY REPRESENTATION OF THE SIMULTANEOUS ROTATION OF THE HEAD AND EYES.

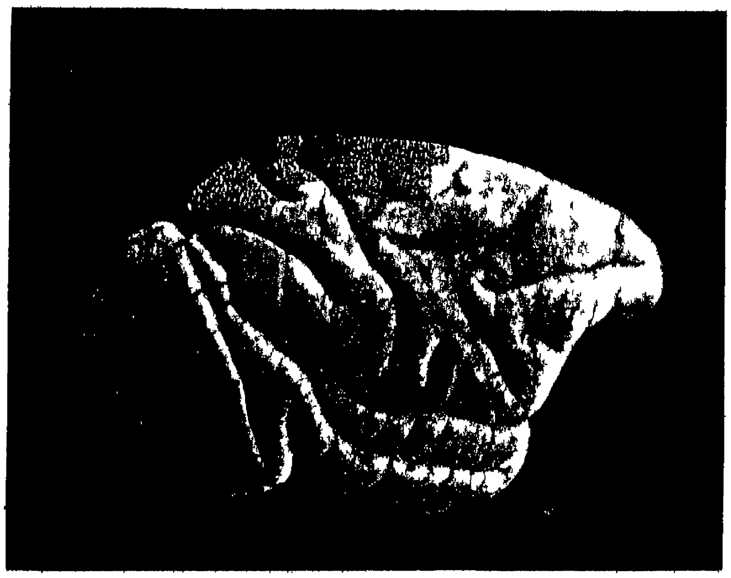
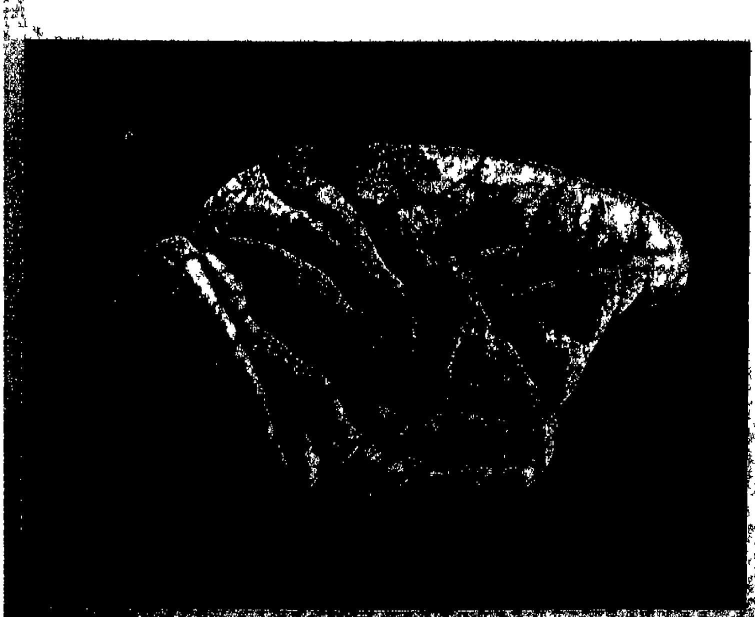


Fig. 6.—ABSOLUTE REPRESENTATION OF THE HALLUX.



PRIMARY REPRESENTATION OF THE HALLUX.

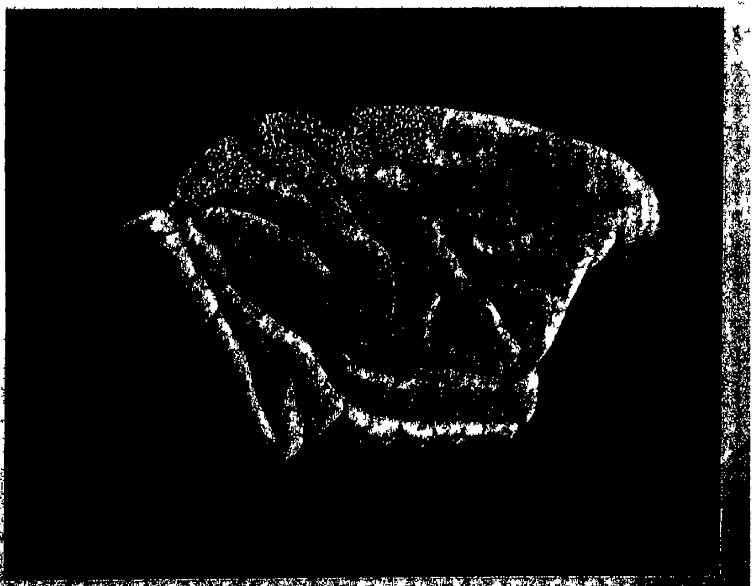


Fig. 7.—ABSOLUTE REPRESENTATION OF ALL TOES.

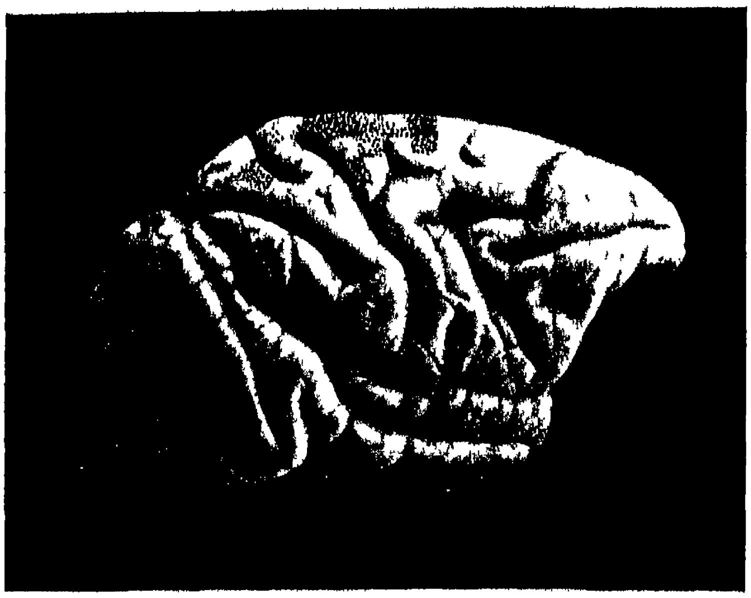


Fig 8.—Representation of the movement of Flexion of All Toes.

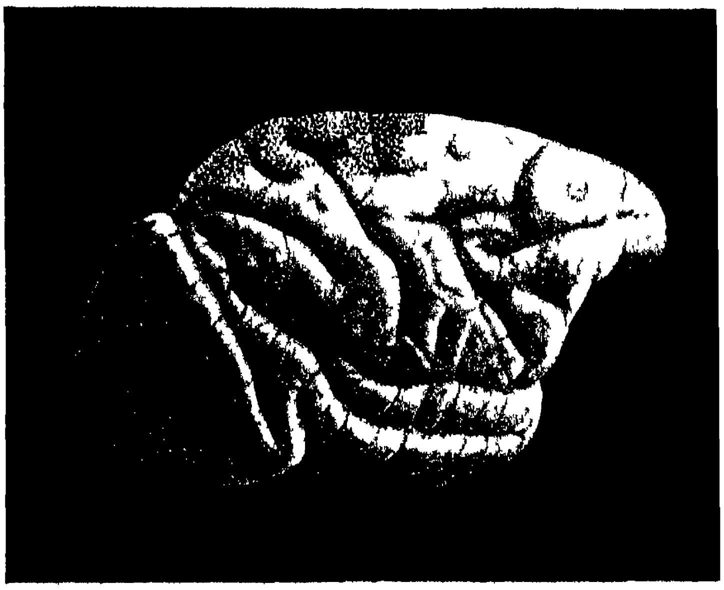


Fig. 9.—Absolute representation of the Small Toes.

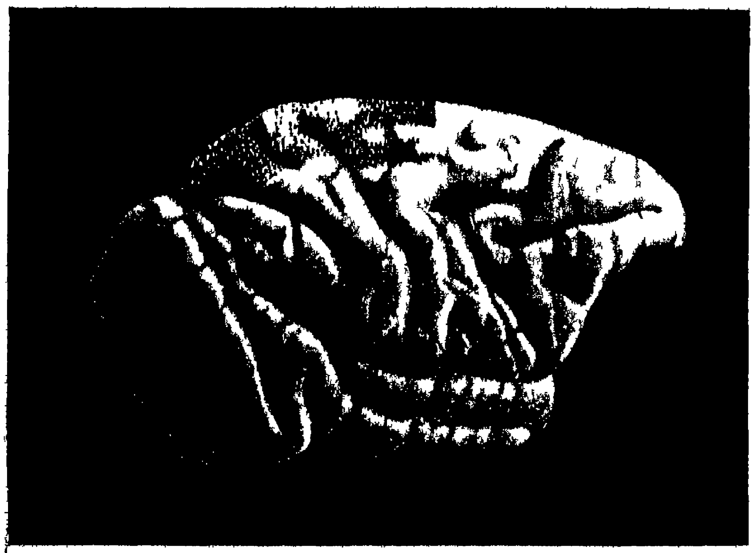


Fig. 10.—Primary representation of the Small Toes.

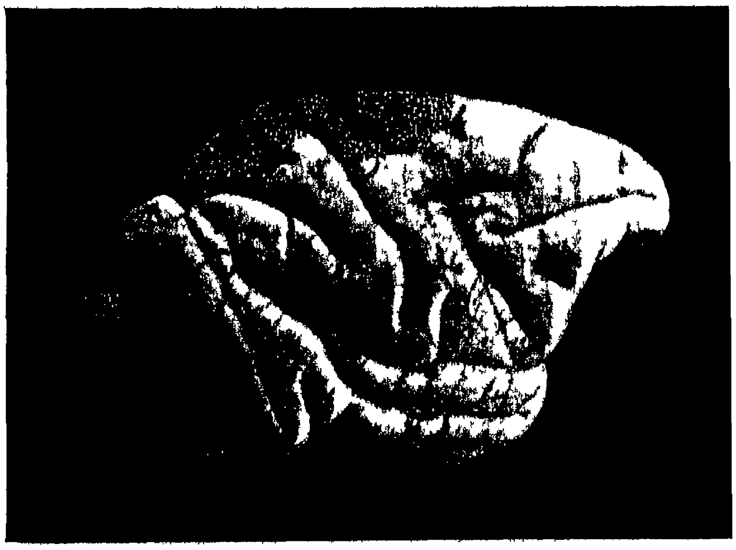


Fig. 11.—Absolute representation of the Ankle.

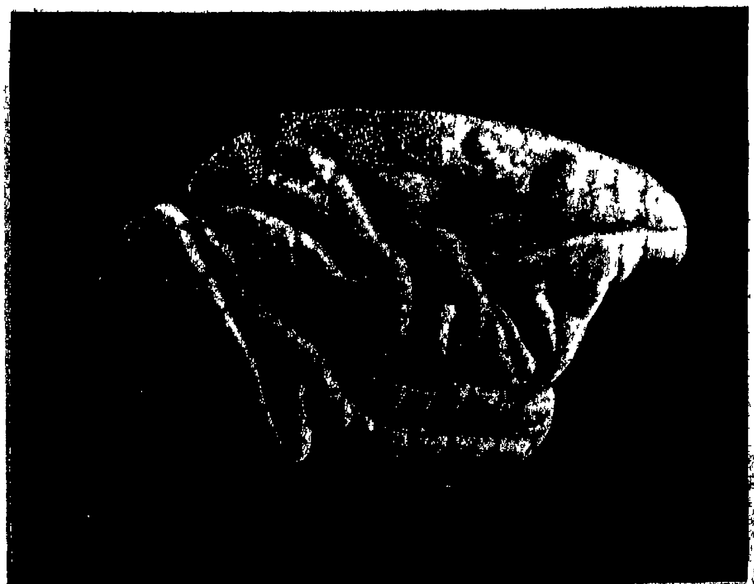


Fig. 12.—Absolute representation of the Knee.

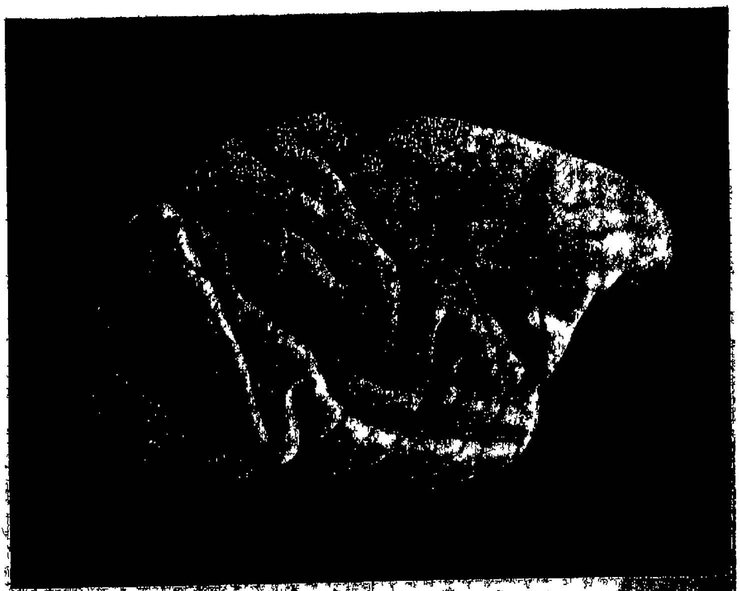


Fig. 13.—Absolute representation of the Hip.

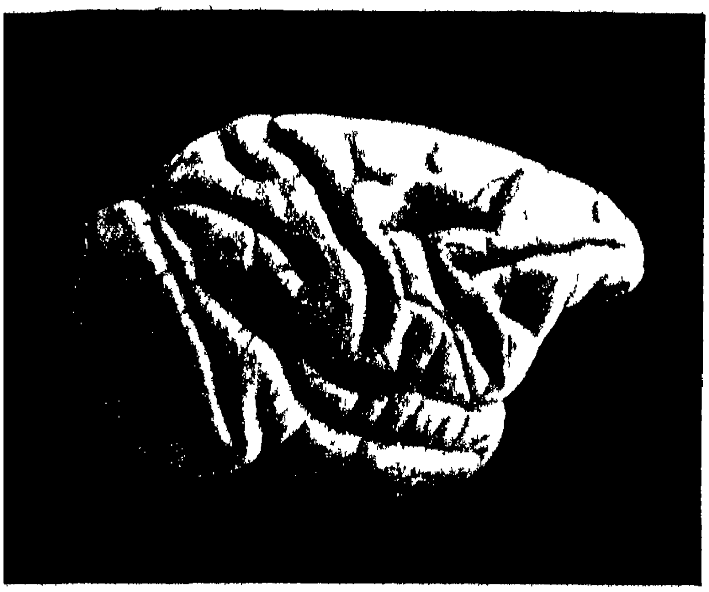


Fig. 16.—Absolute representation of the Thumb.

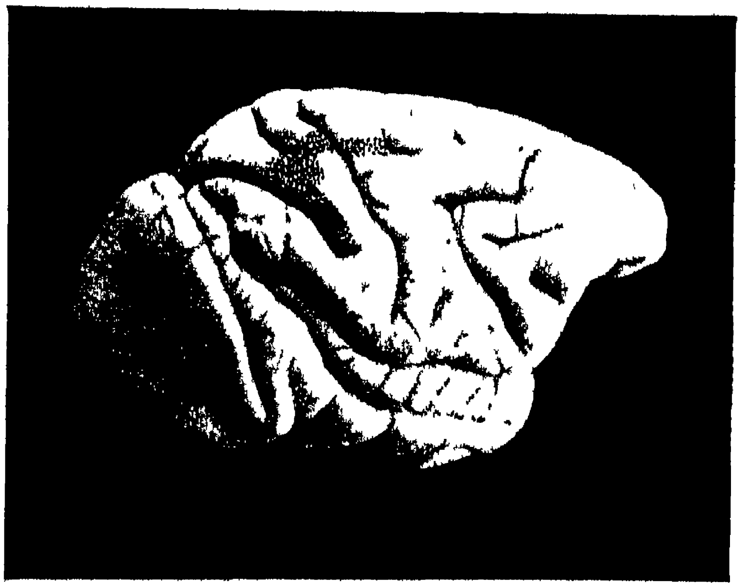


Fig. 17.—Absolute representation of the Fingers.

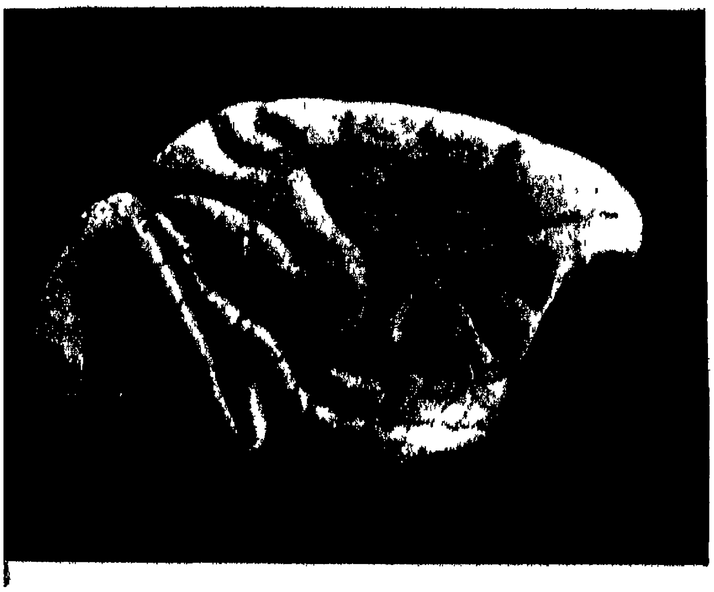


Fig 18.—Absolute representation of the Wrist.

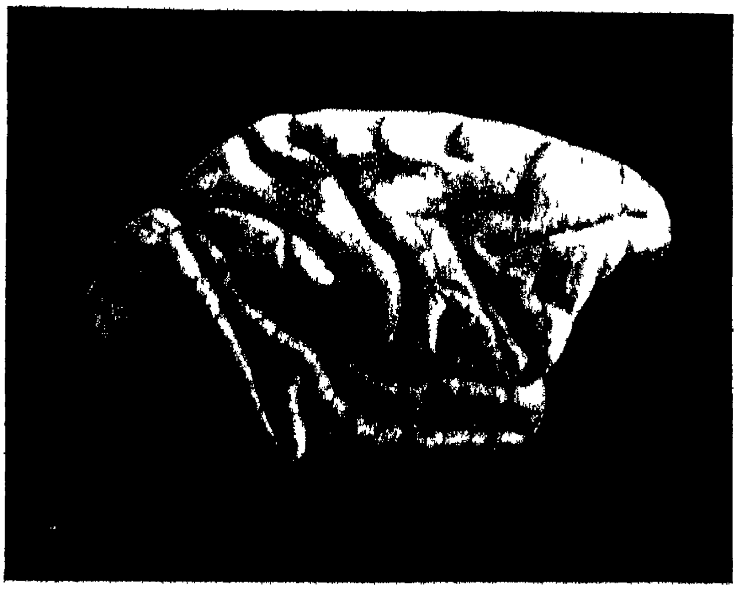


Fig. 19.—Absolute representation of the Elbow.

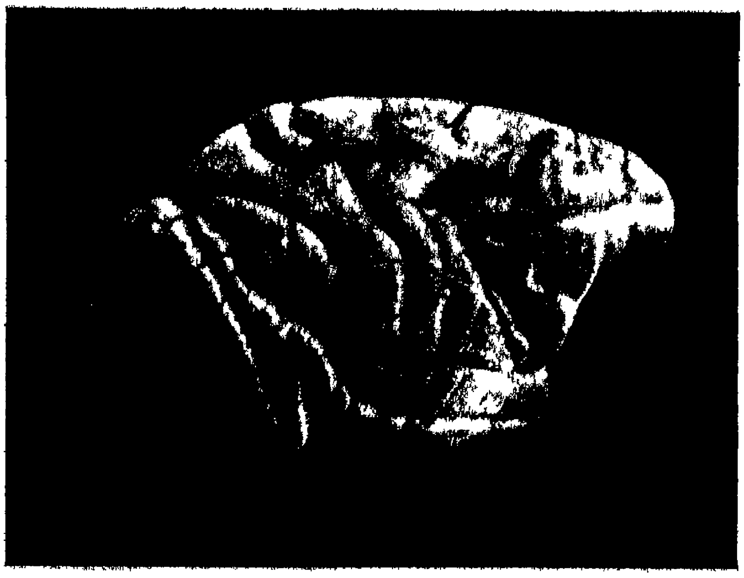


Fig. 20.—Absolute representation of the Shoulder.

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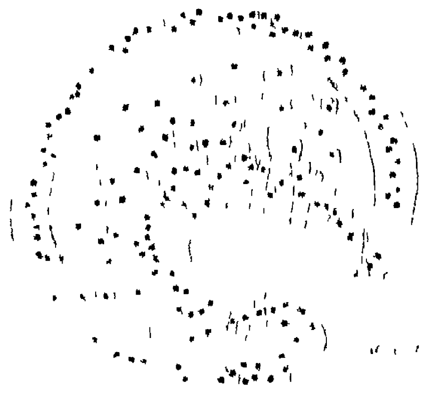

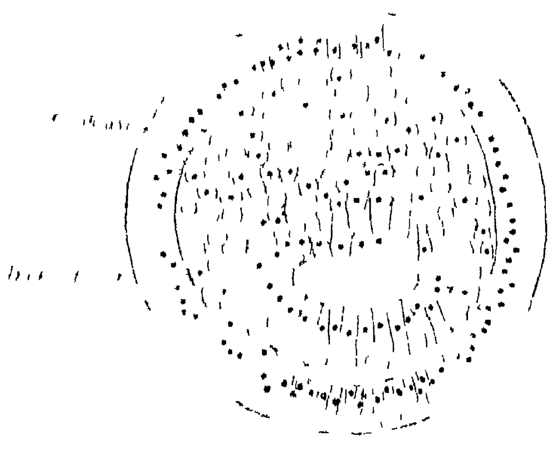

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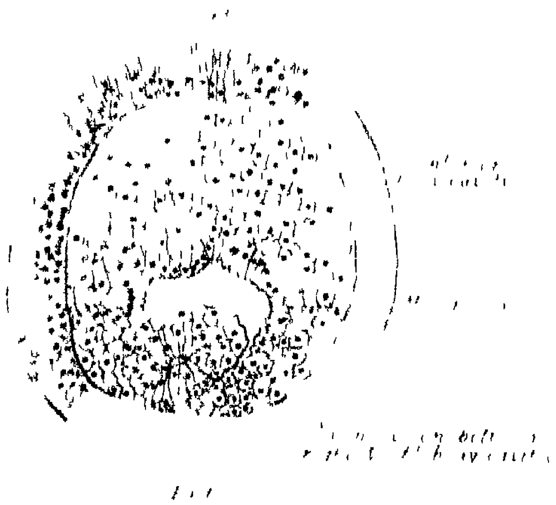
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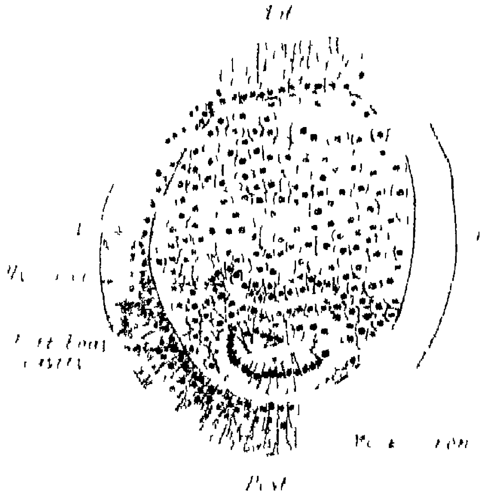
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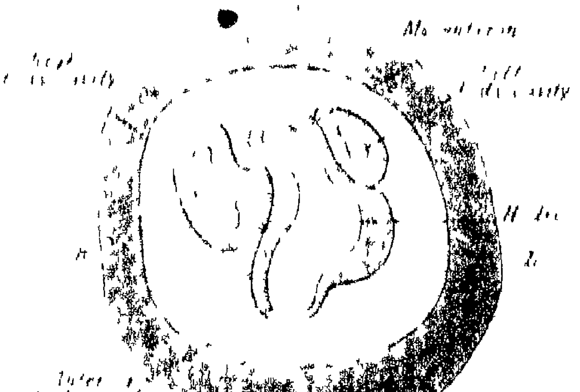
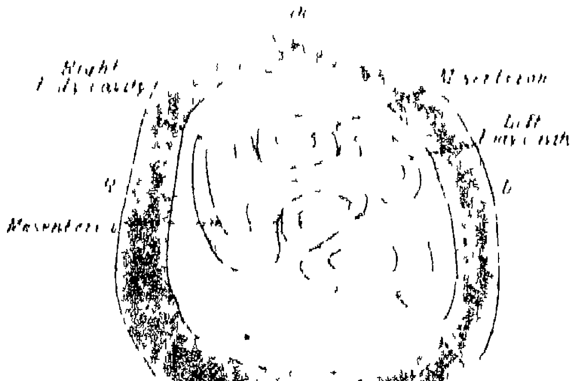

Mesenteron
Left body cavity
Right body cavity
H
L
V

8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Mesenteron
Left body cavity
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L
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V

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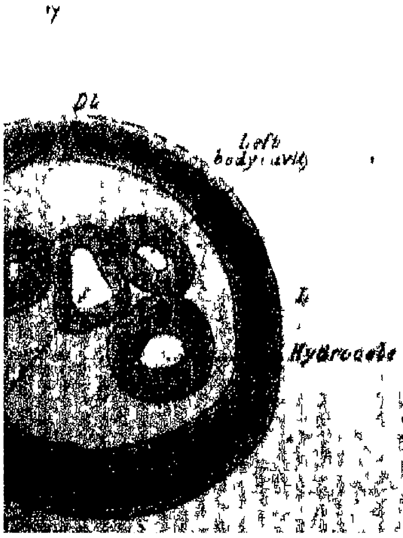
Dl
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L
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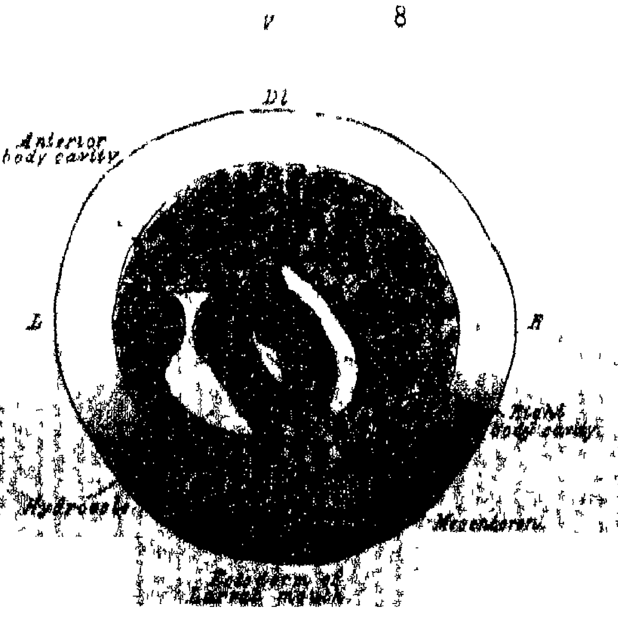
Dl
Anterior body cavity
L
R
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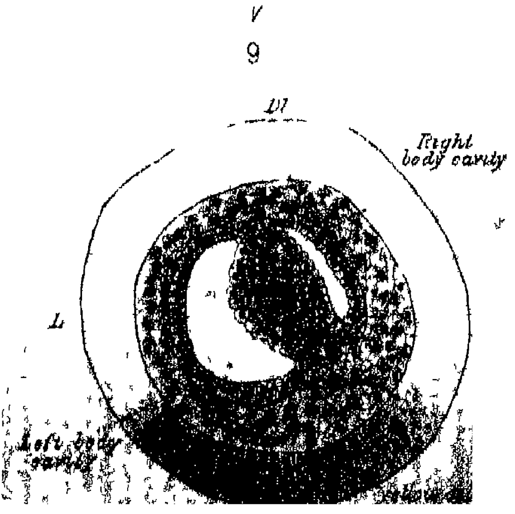
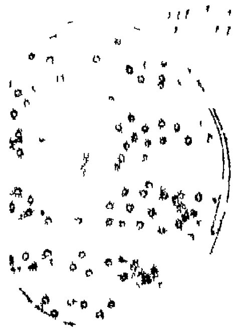
Hydrocoele
Mesentery


Dl
Right body cavity
L
Left body cavity



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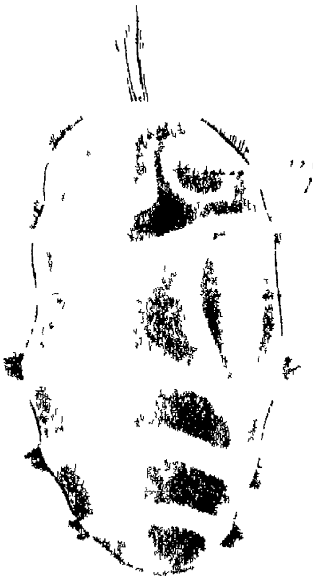

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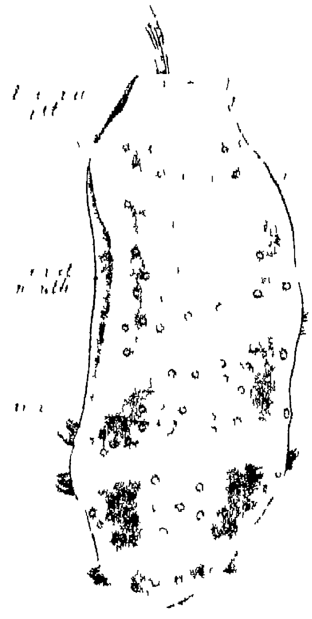

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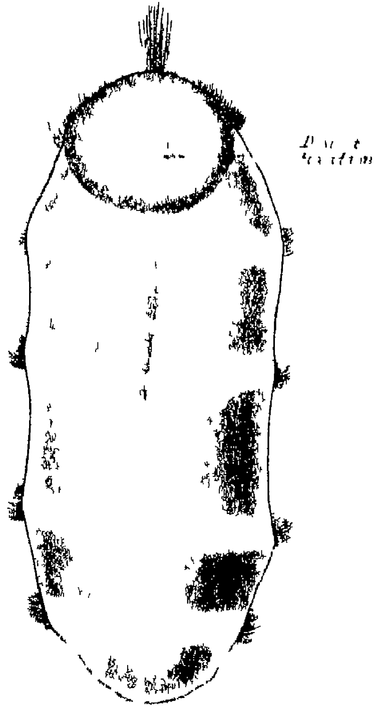

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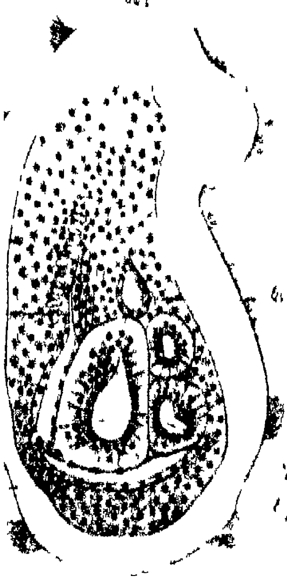

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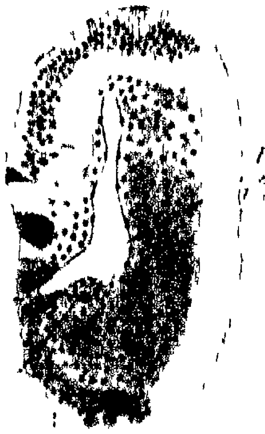

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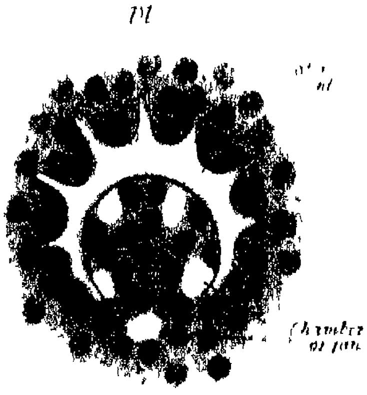

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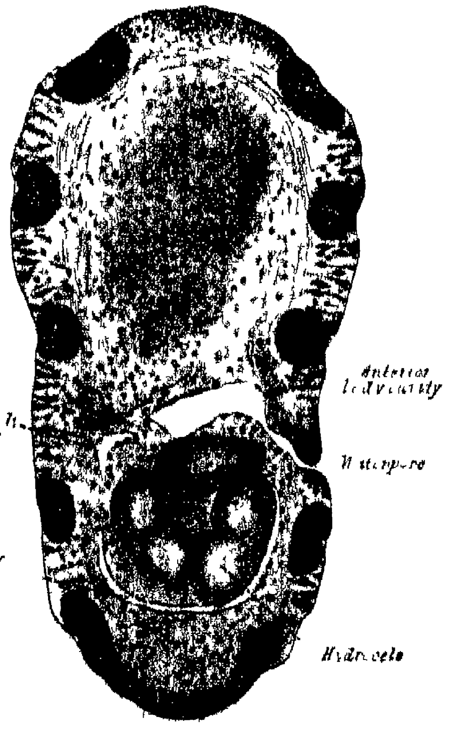

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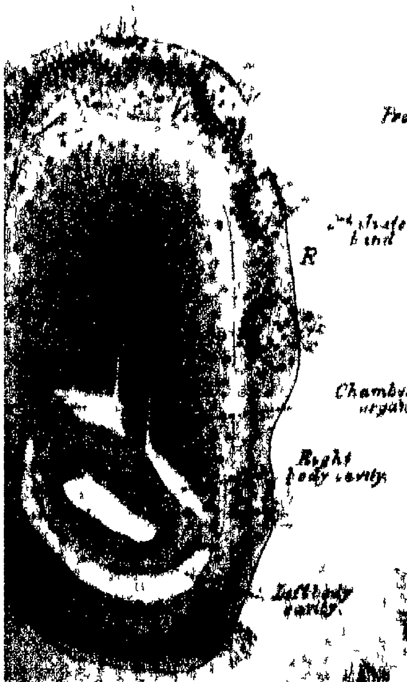

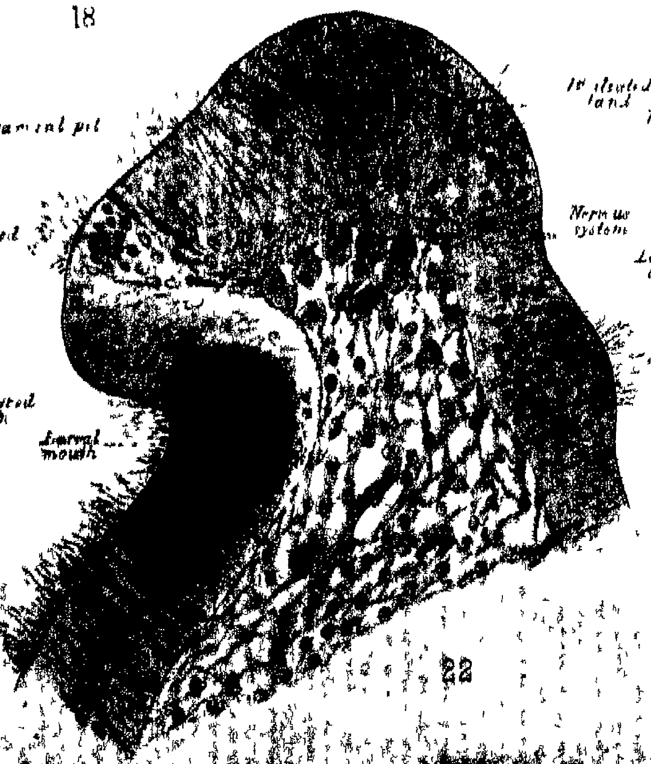

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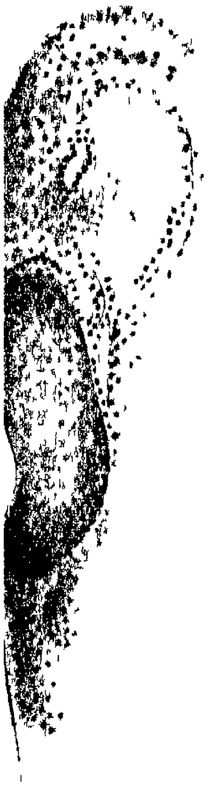

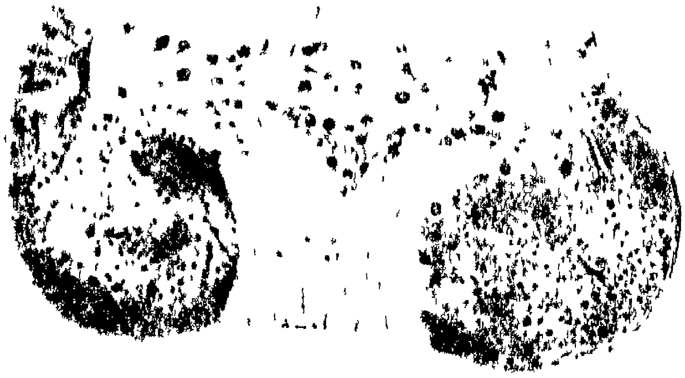

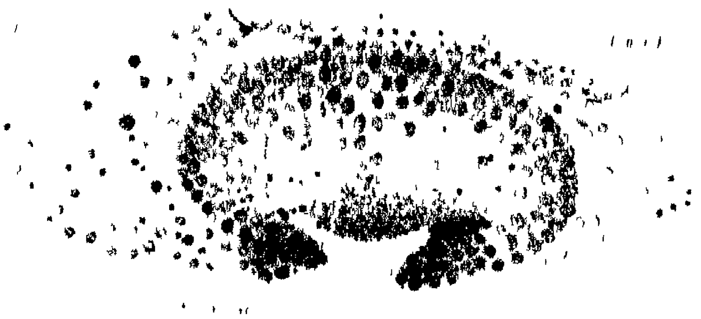

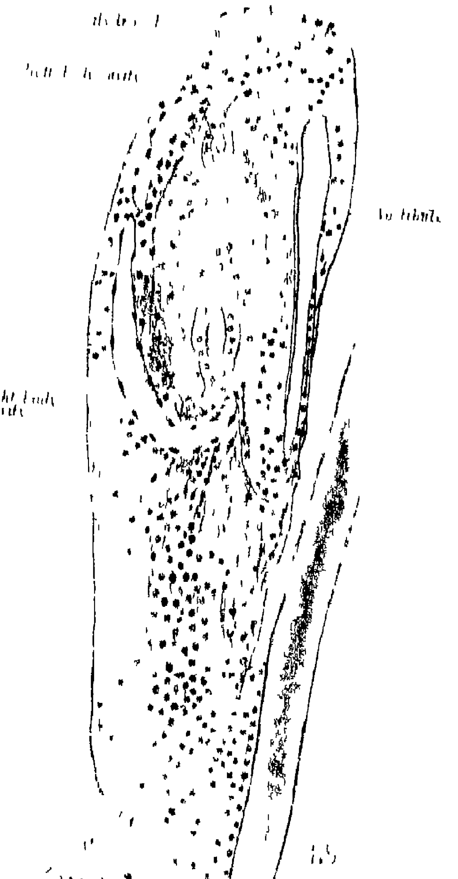

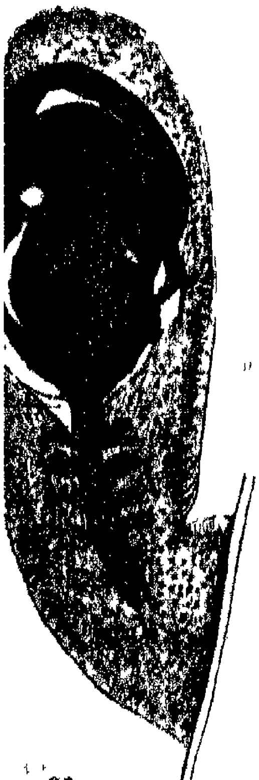

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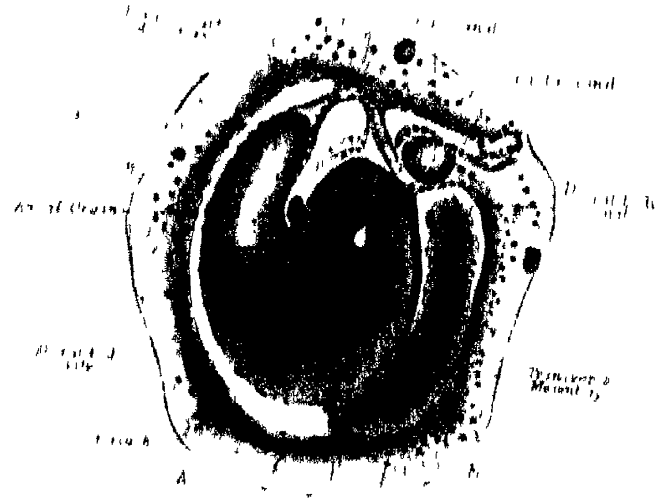
A

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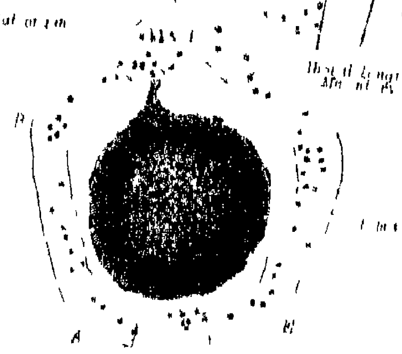
Axial organ
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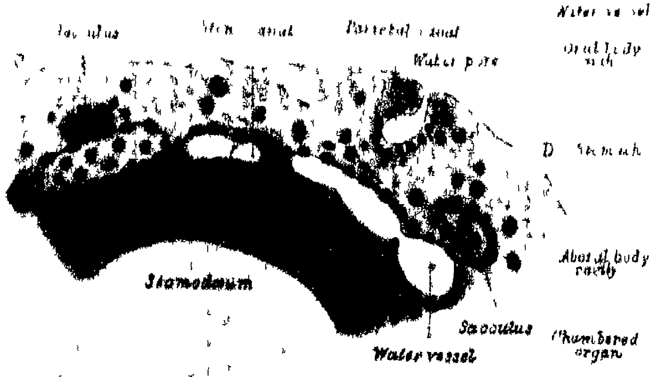
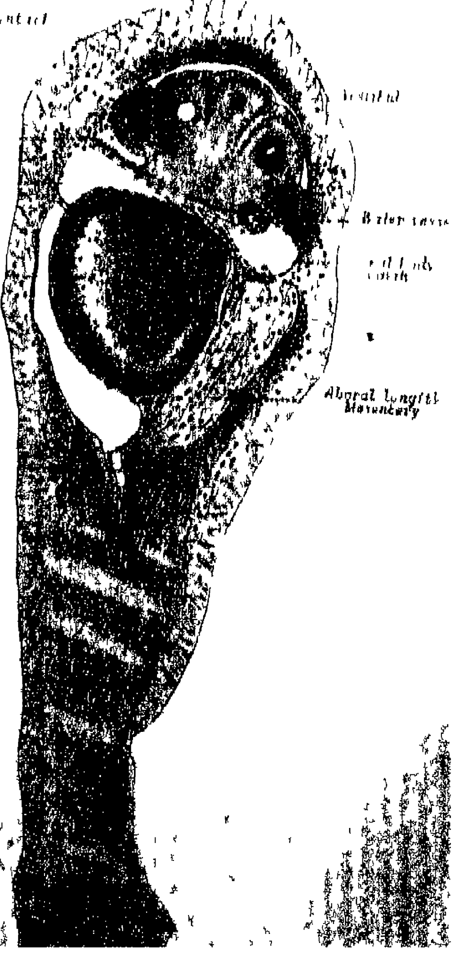
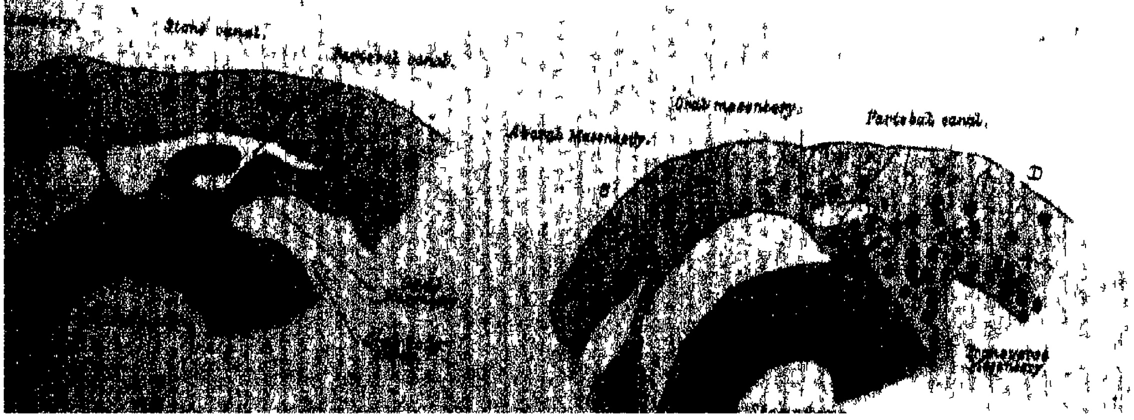

Parietal canal
Water pore
Stomodaeum
Saccculus
Water vessel

32


Tentacle
Water vessel
Oral body cavity
D Stomach
Aboral body cavity
Chambered organ
Water vessel
Aboral Longitl Mesentery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Parietal canal
Oral mesentery
Aboral Mesentery
Parietal canal
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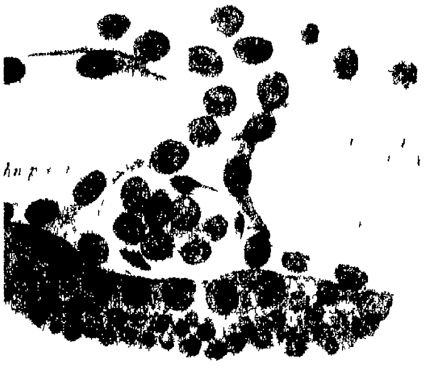

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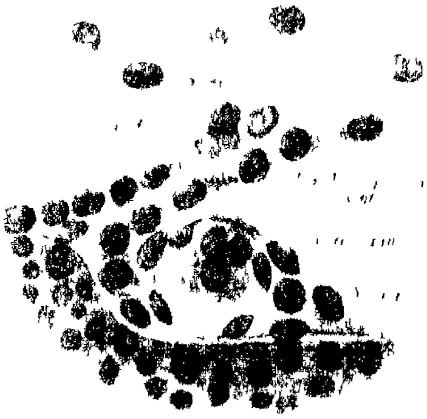

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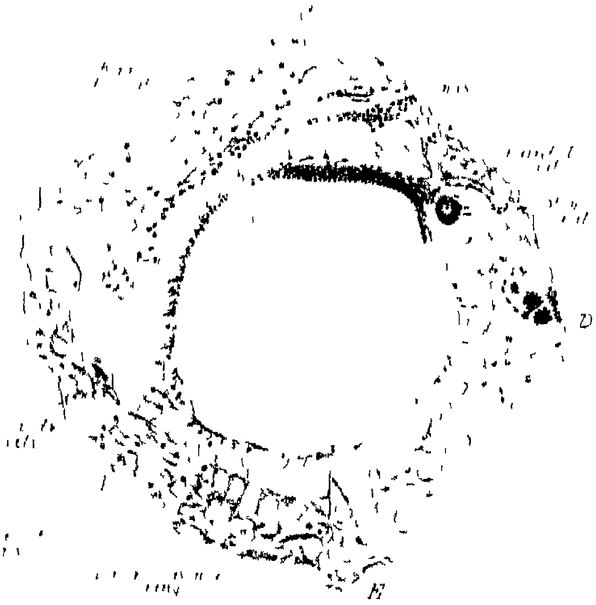

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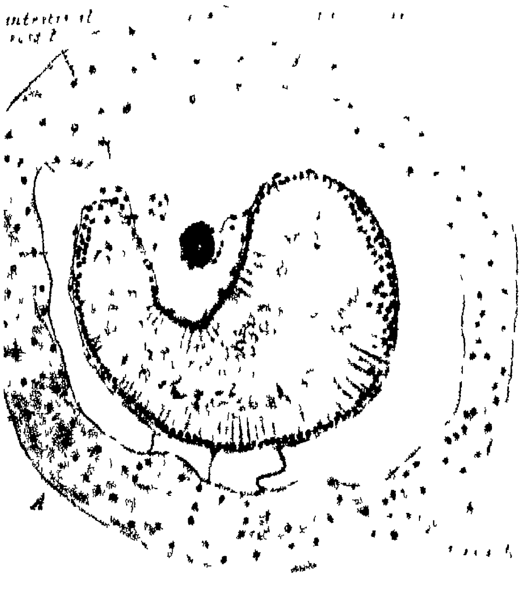

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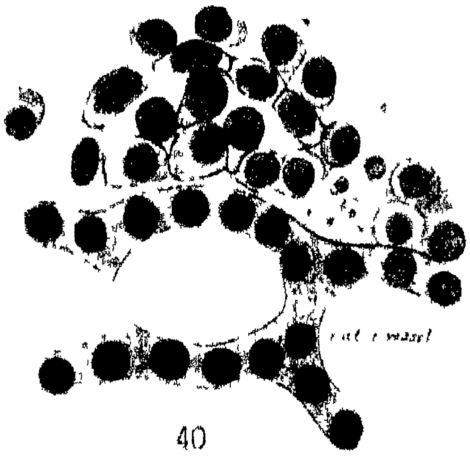

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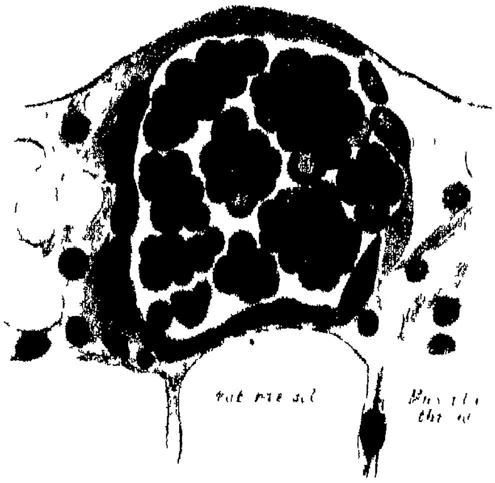

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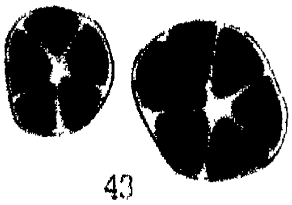

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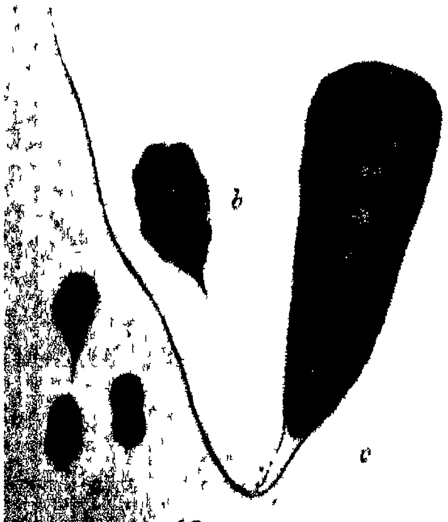

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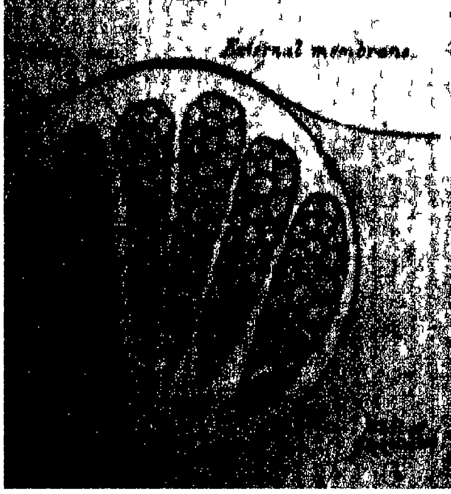
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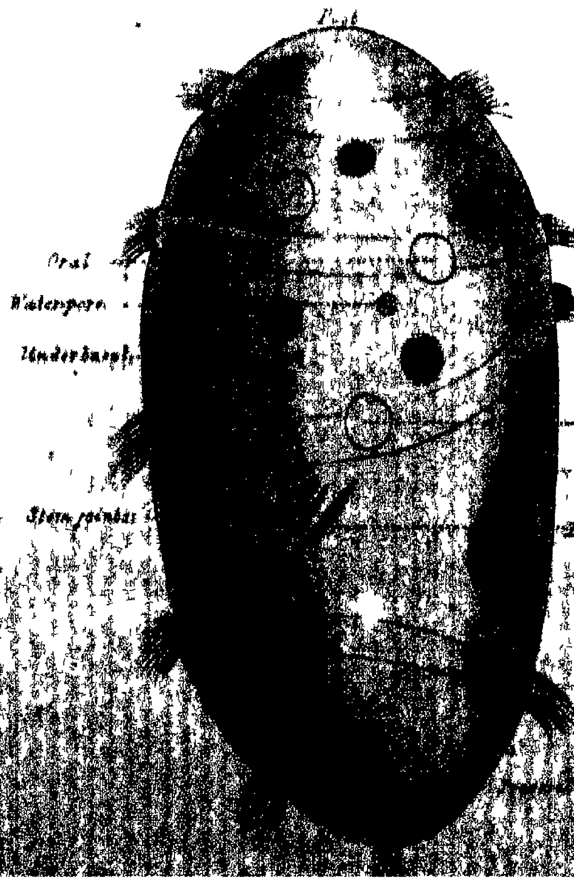

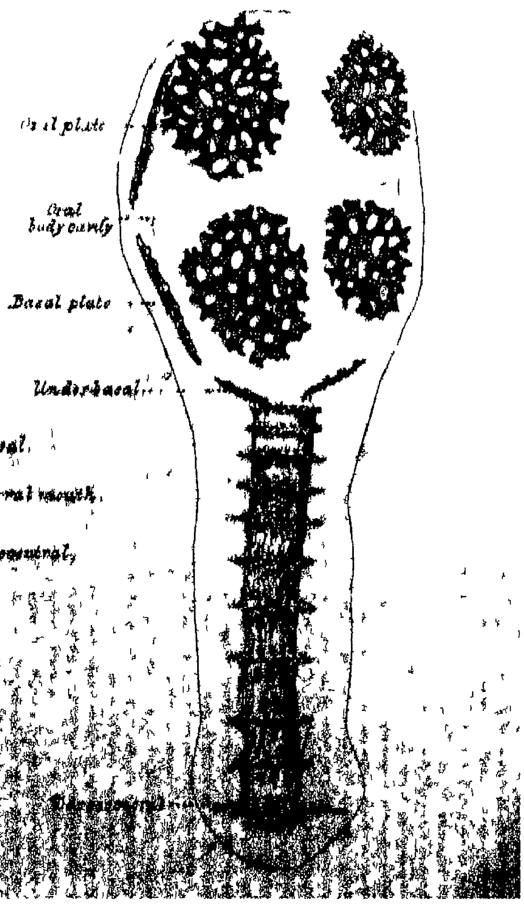

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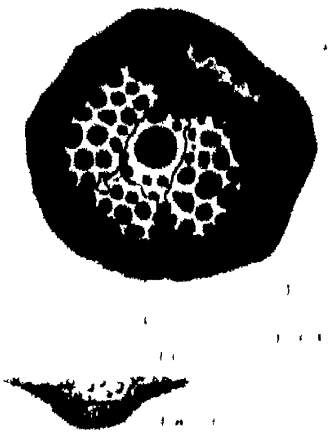

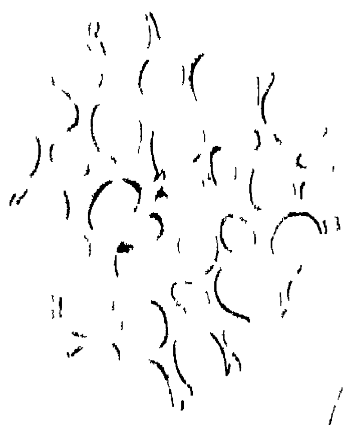

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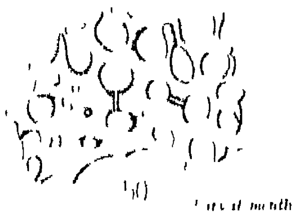

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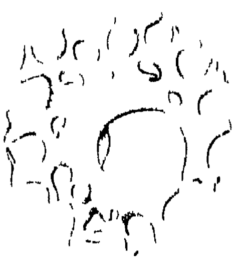

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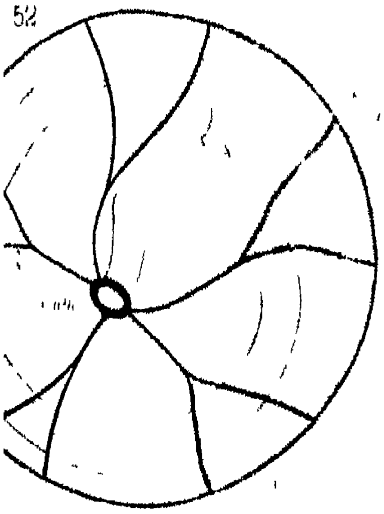

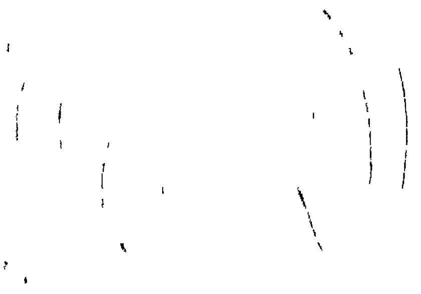

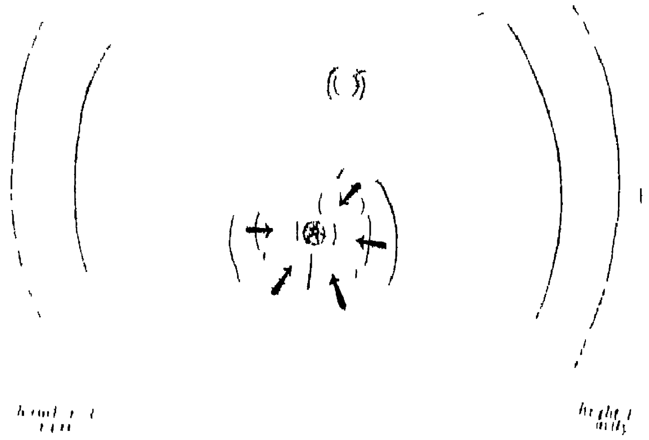

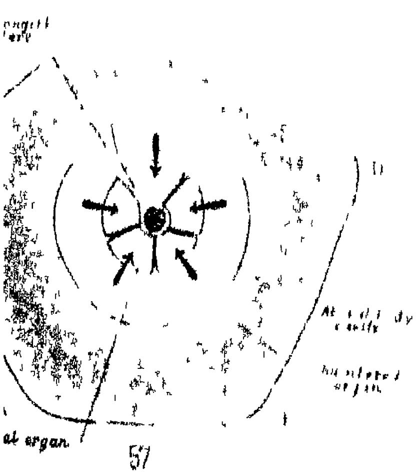

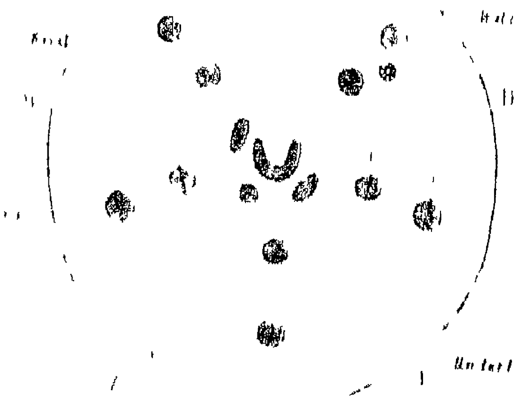

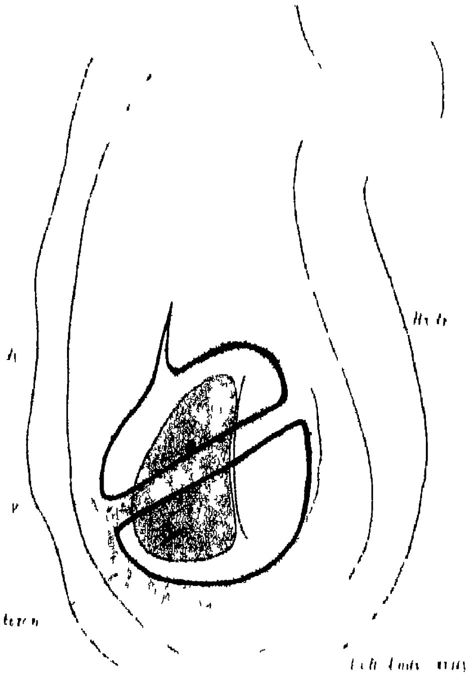

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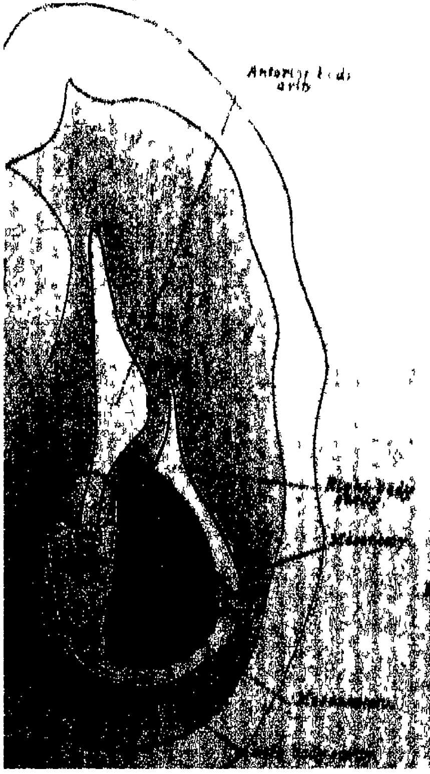

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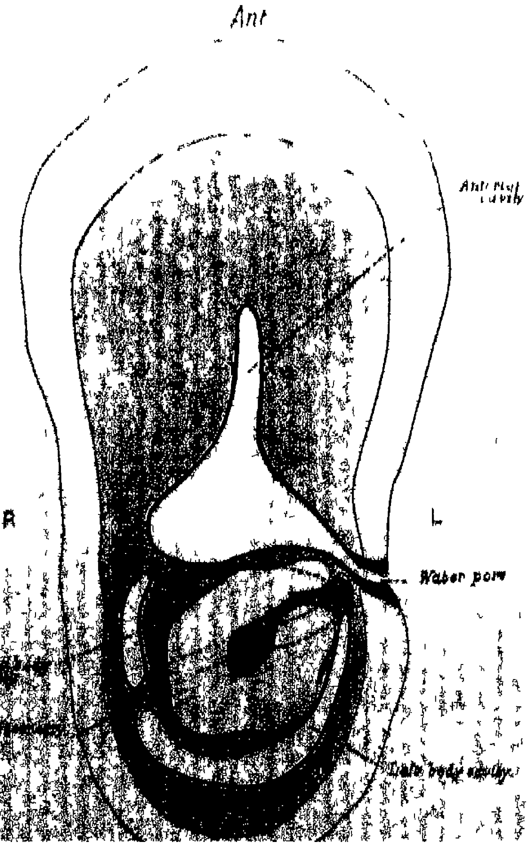

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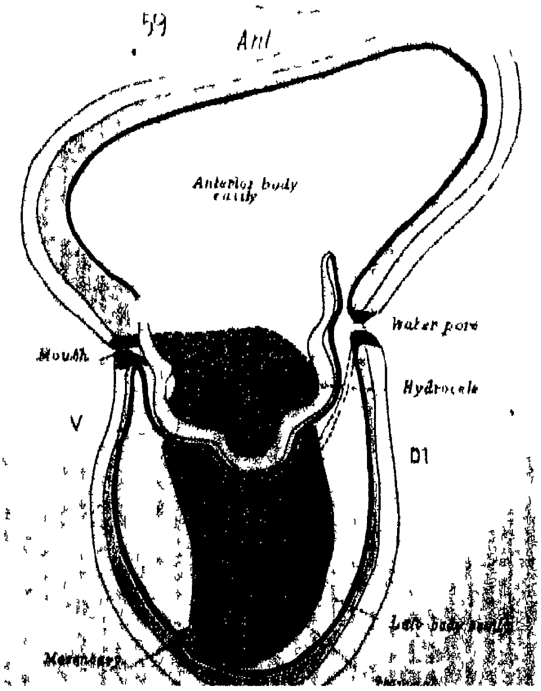

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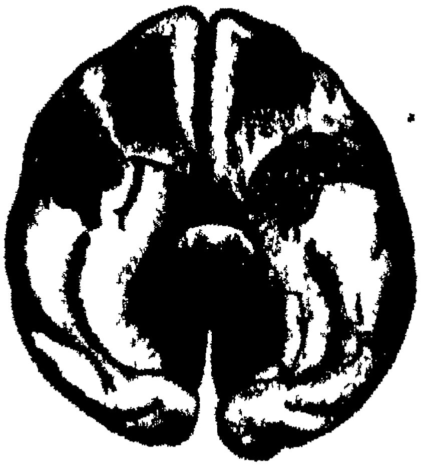

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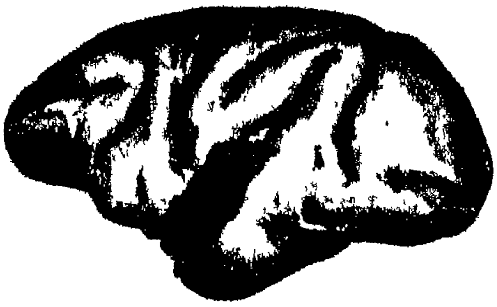

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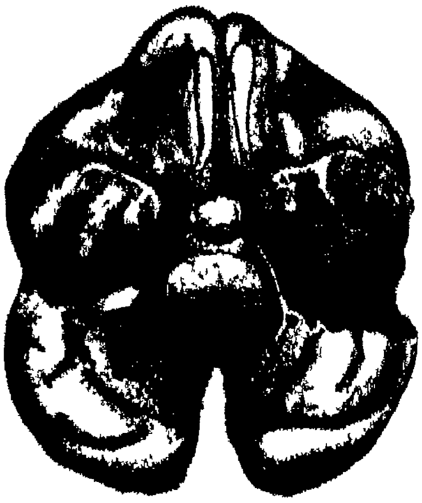

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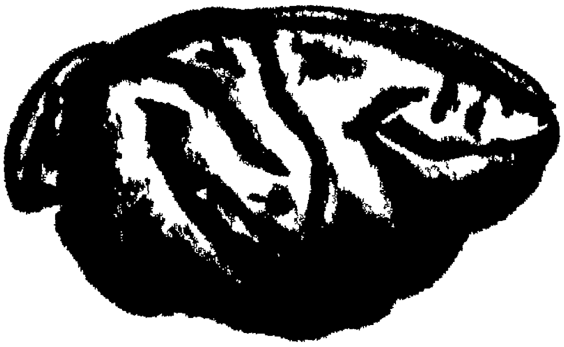

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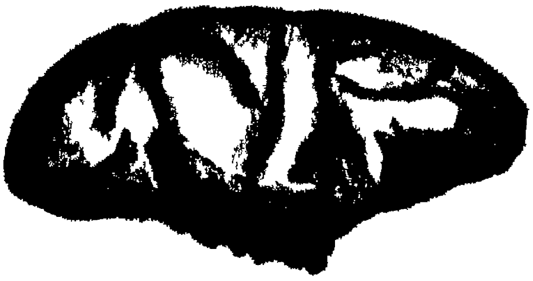

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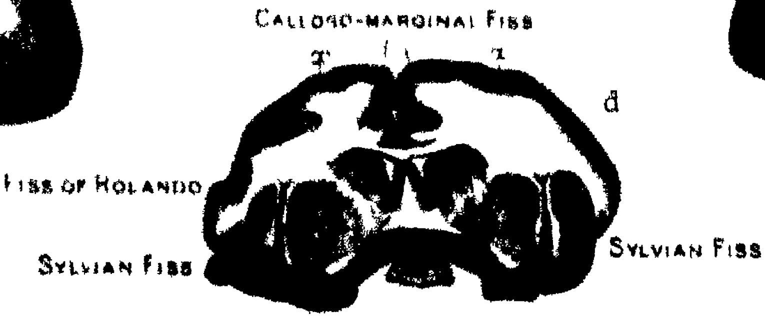

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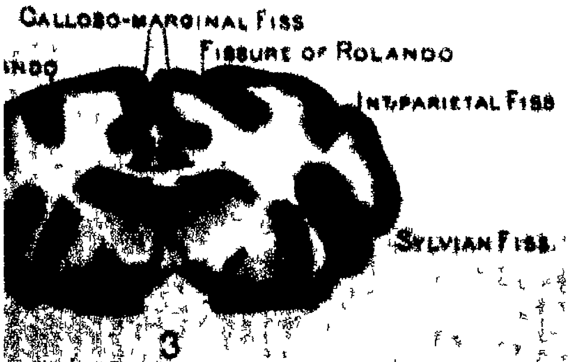

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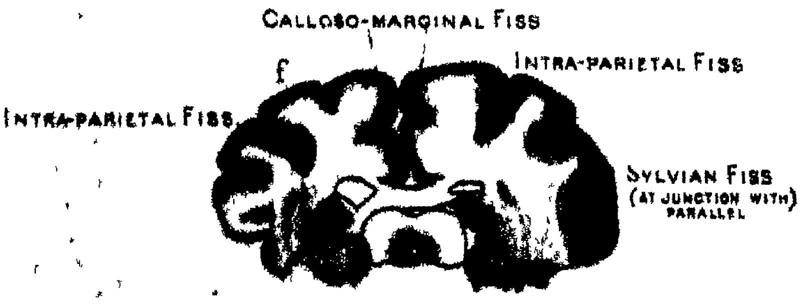

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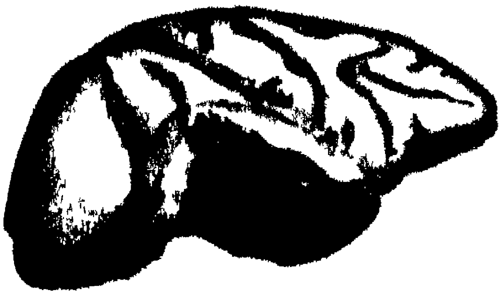

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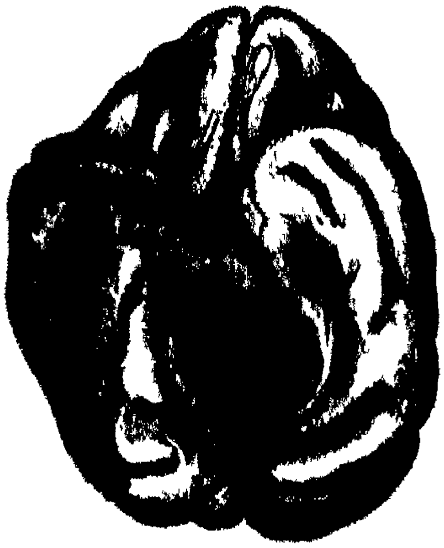

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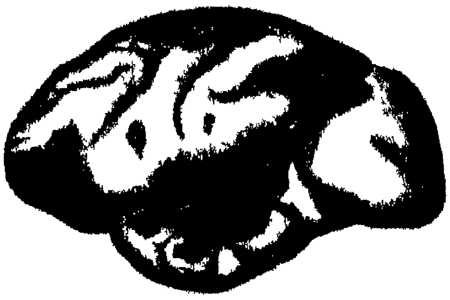

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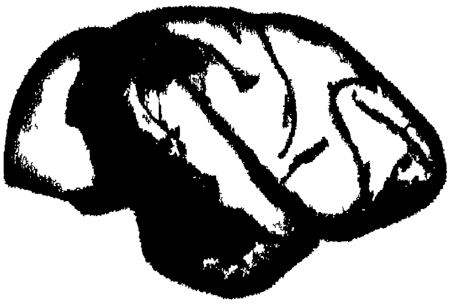

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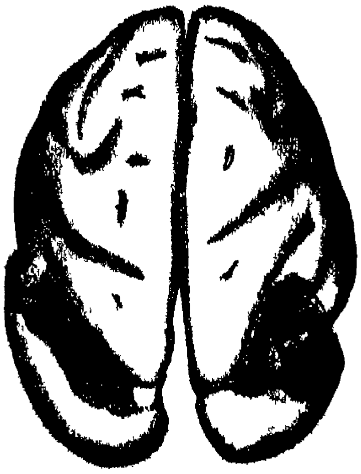

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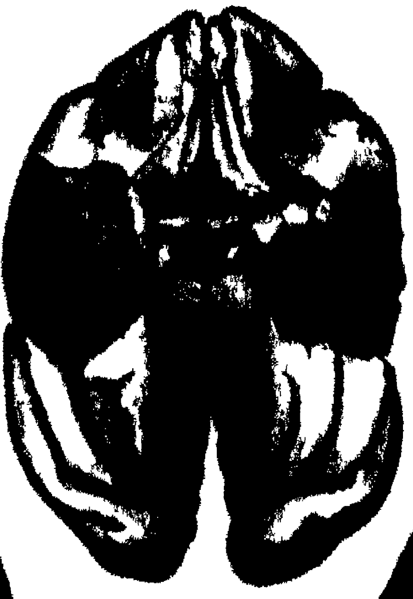

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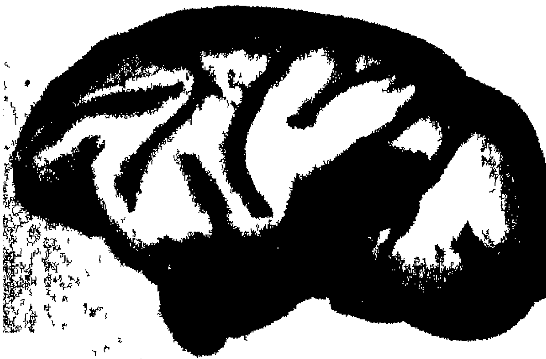

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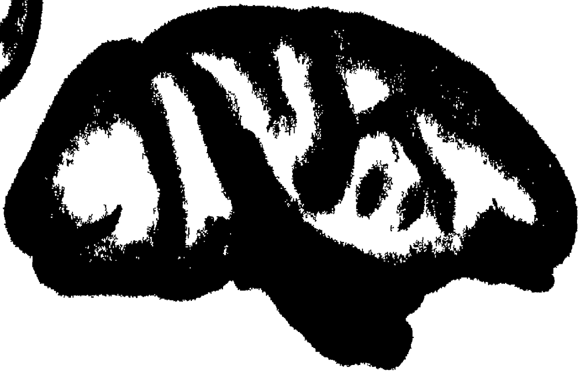

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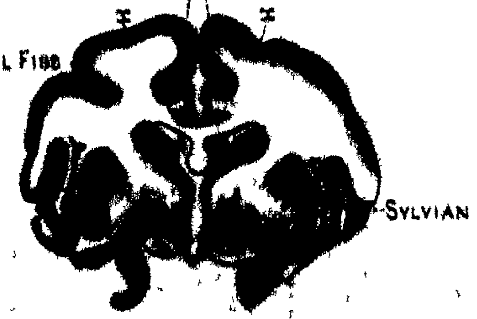

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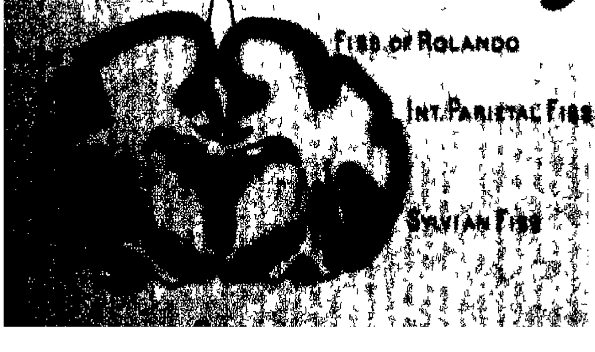

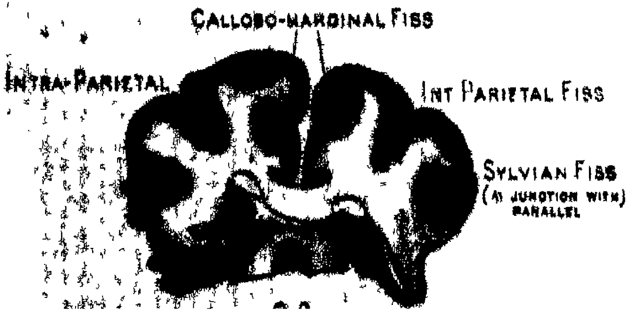

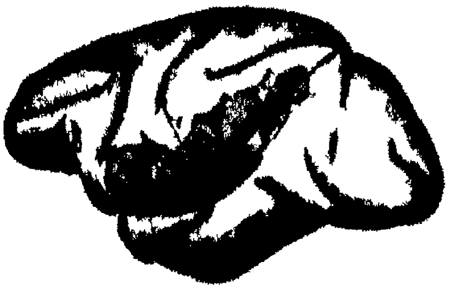

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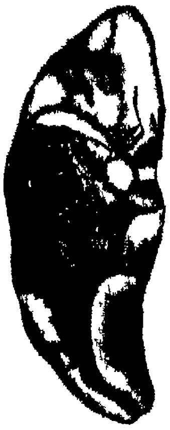

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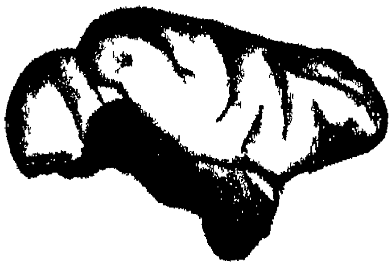

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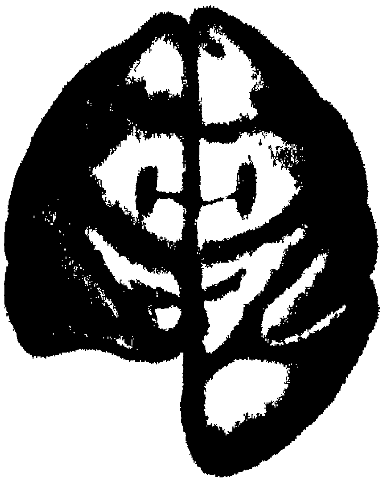

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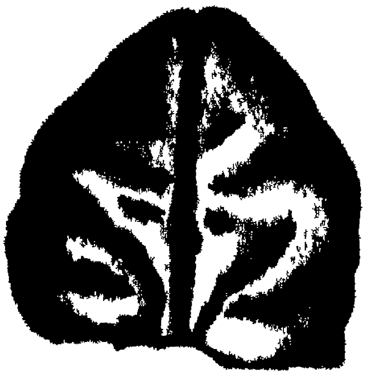

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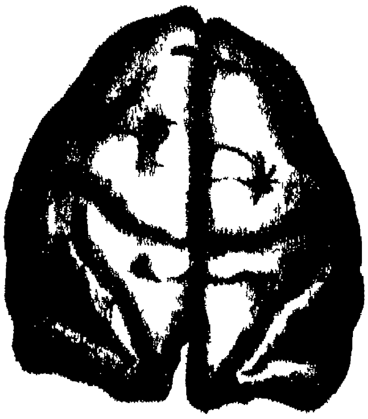
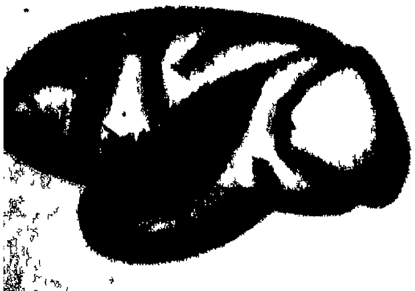


10 a



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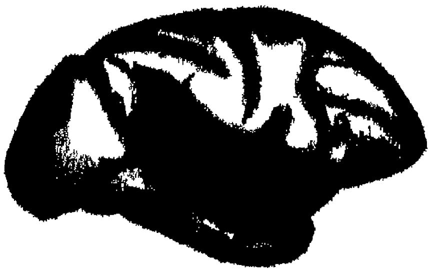

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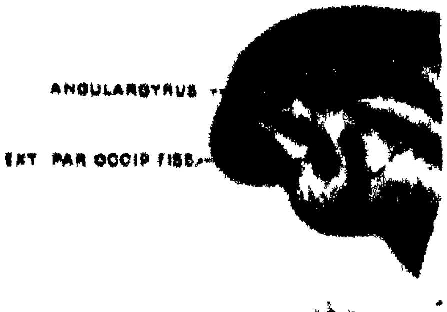

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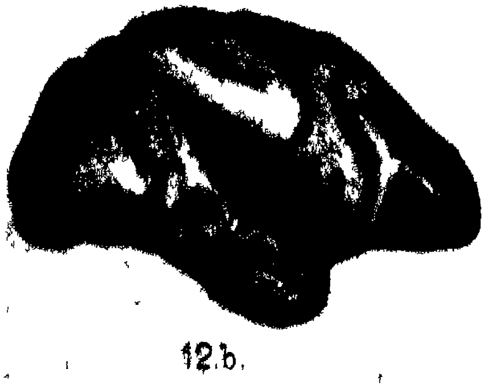

12.b.

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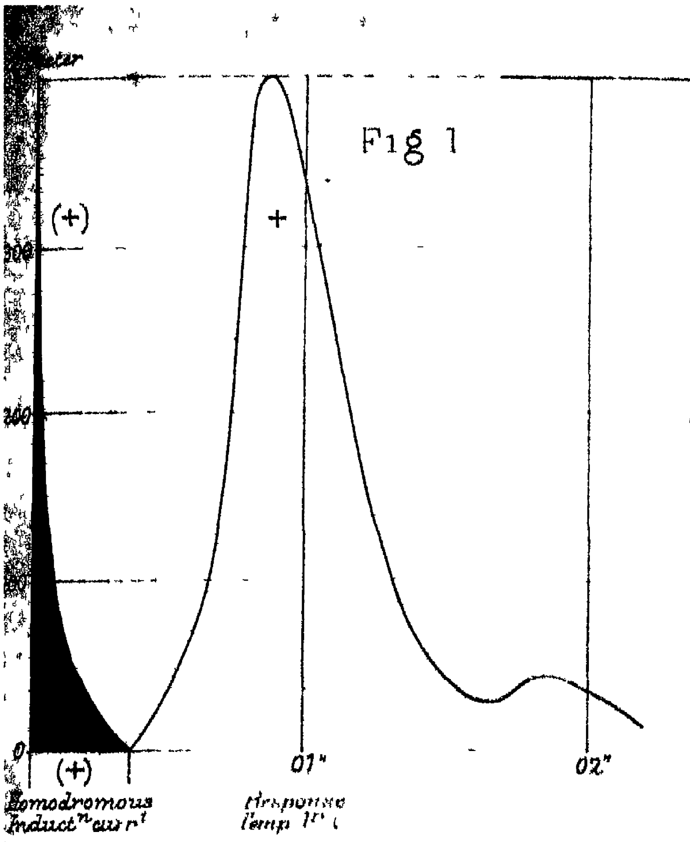


Fig 1

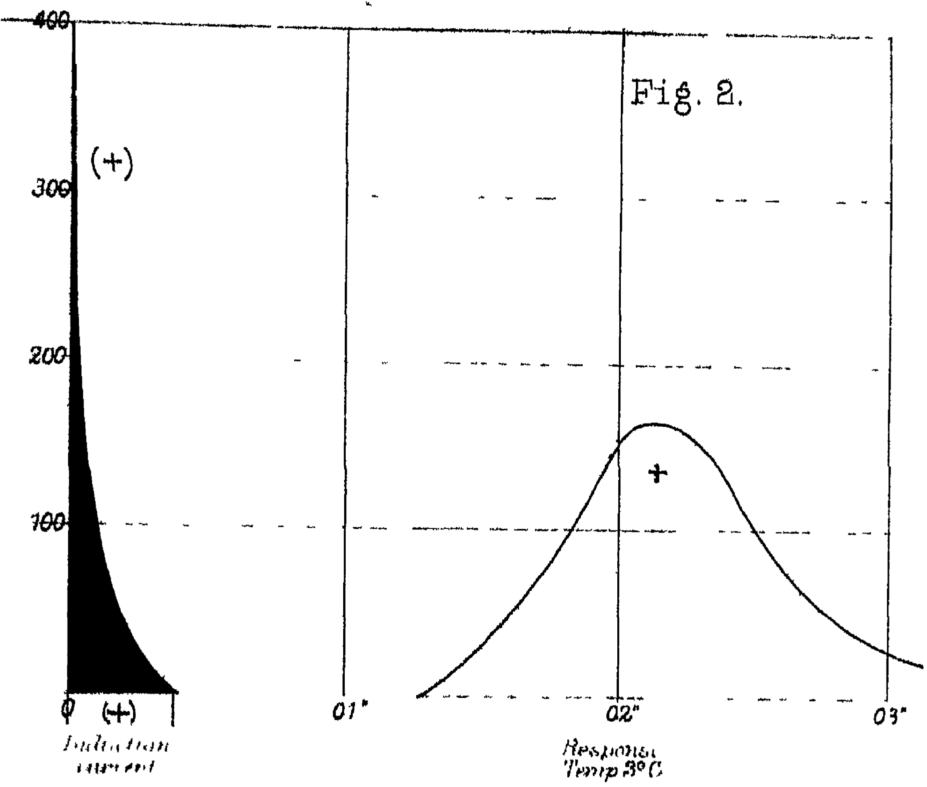


Fig. 2.

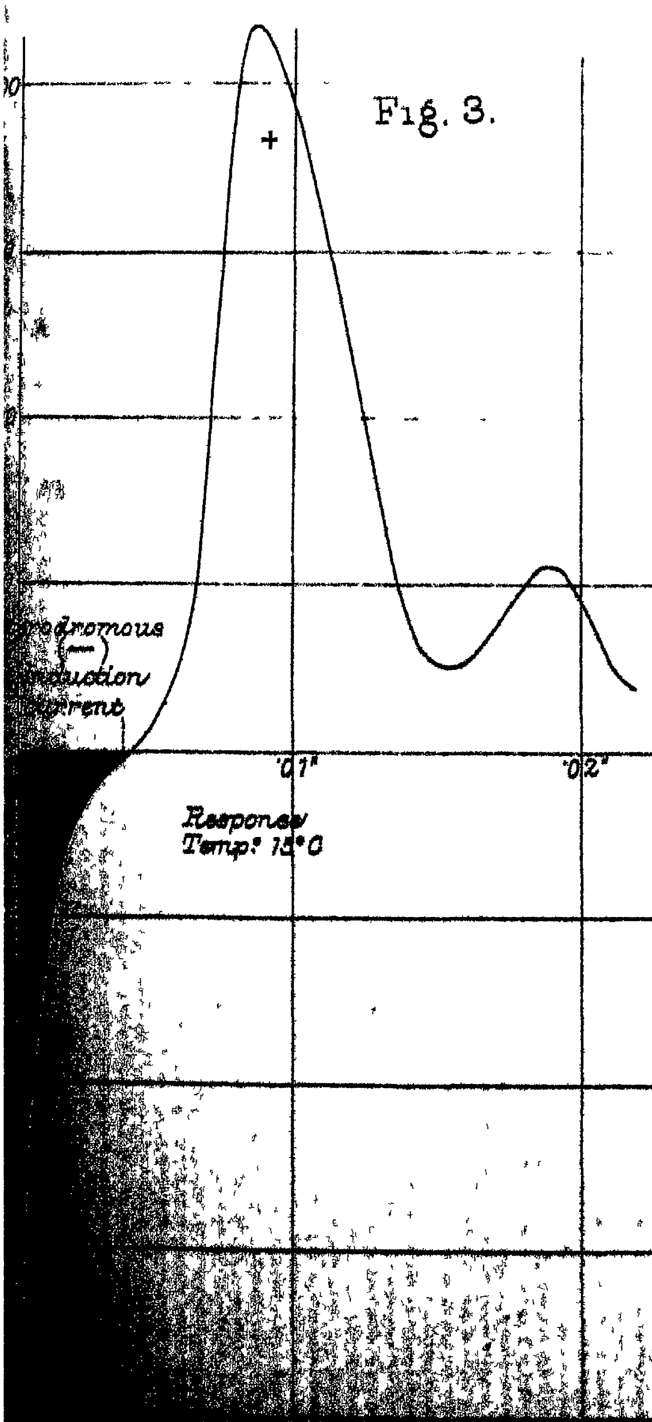


Fig. 3.

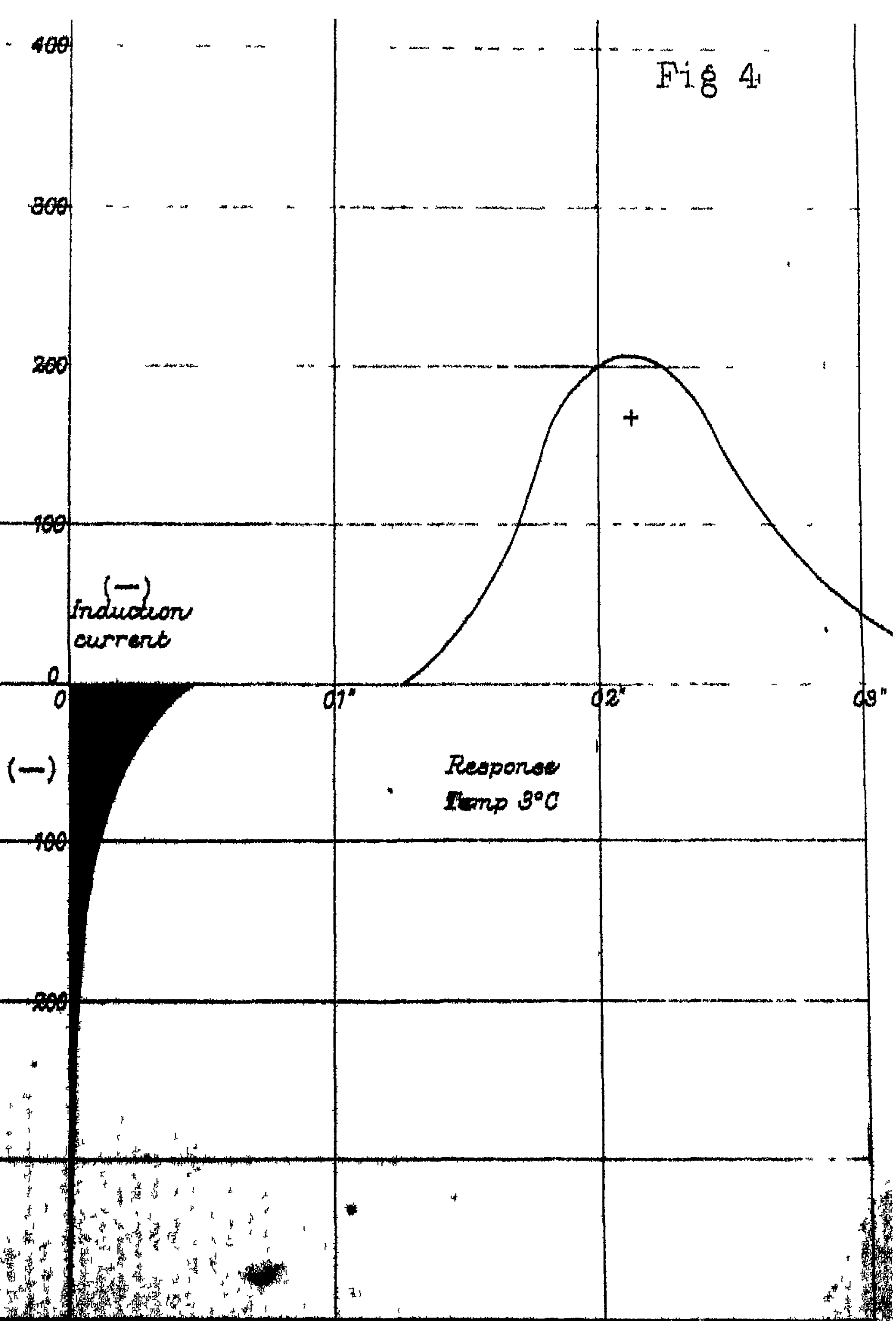
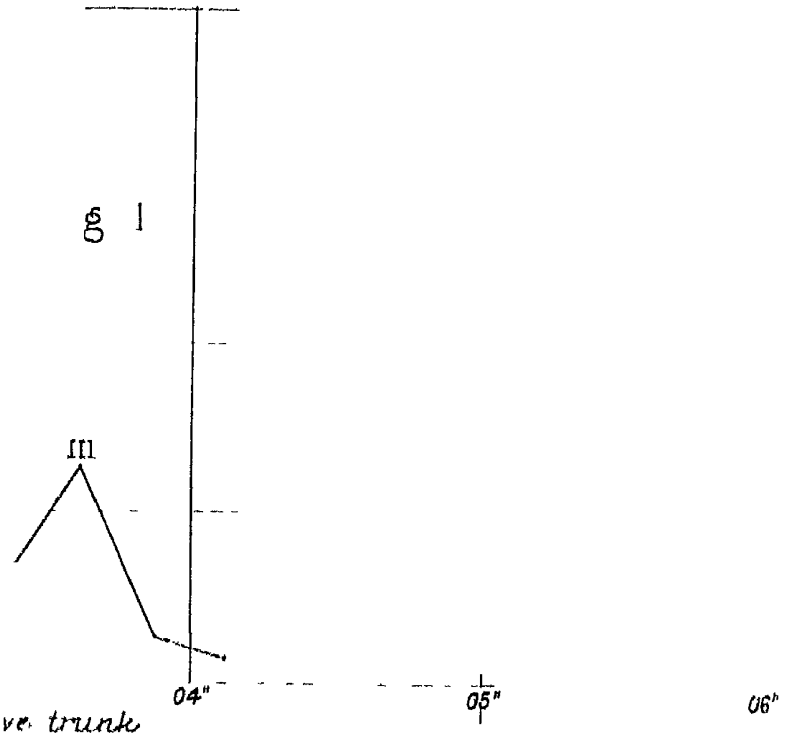


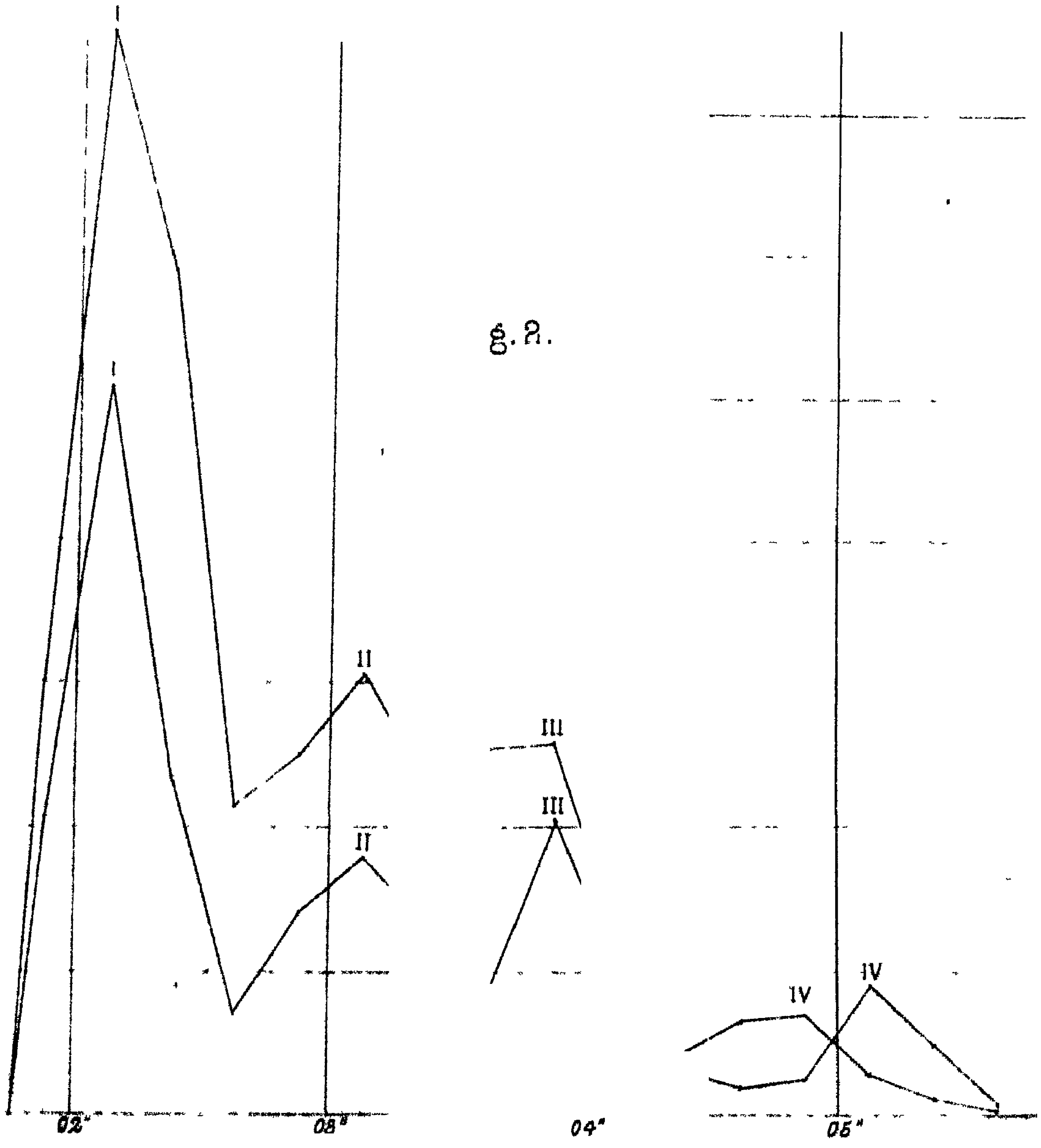
Fig 4

[illegible] through the columns of an Induction current.

West, Newman & Co. lith.

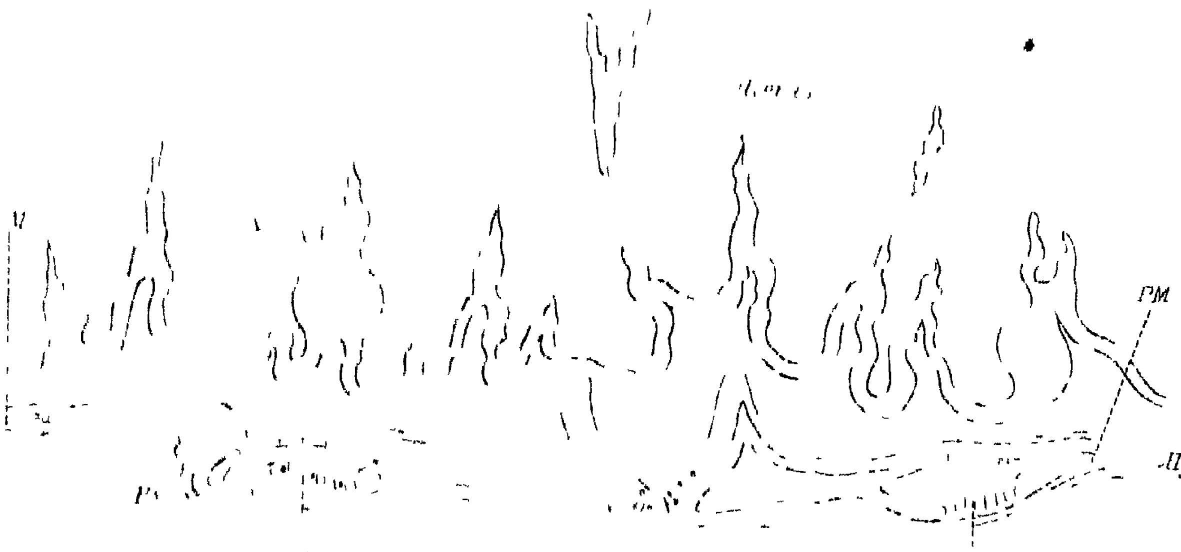


u after excitation of nerve trunk

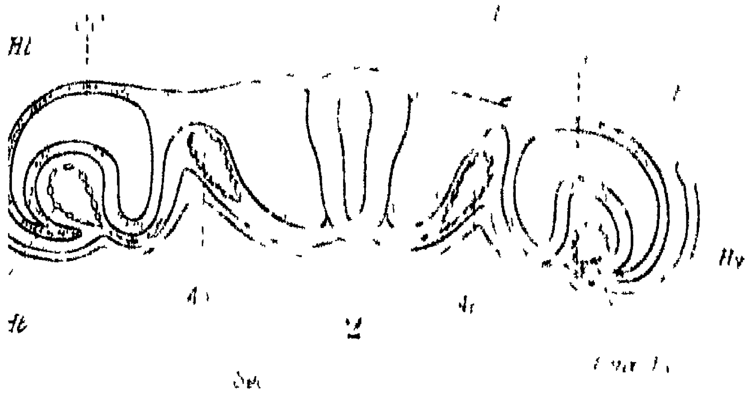


Electrical response of nerve organ preparations to single excitation of nerve showing primary, secondary, tertiary &c. responses

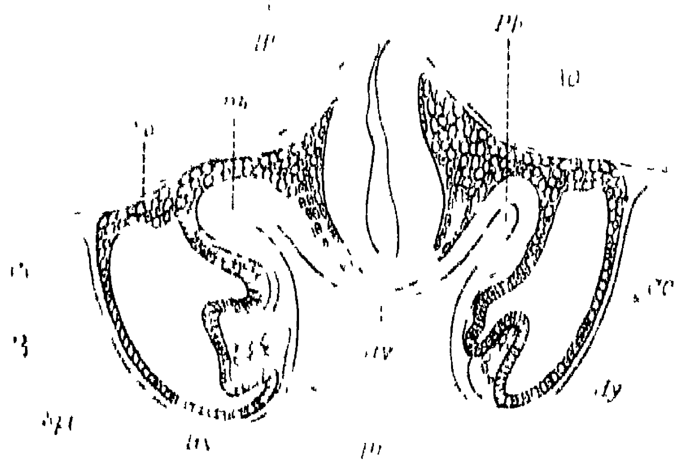
West, Newman & Co lith.


V
PM
Hy
Pr

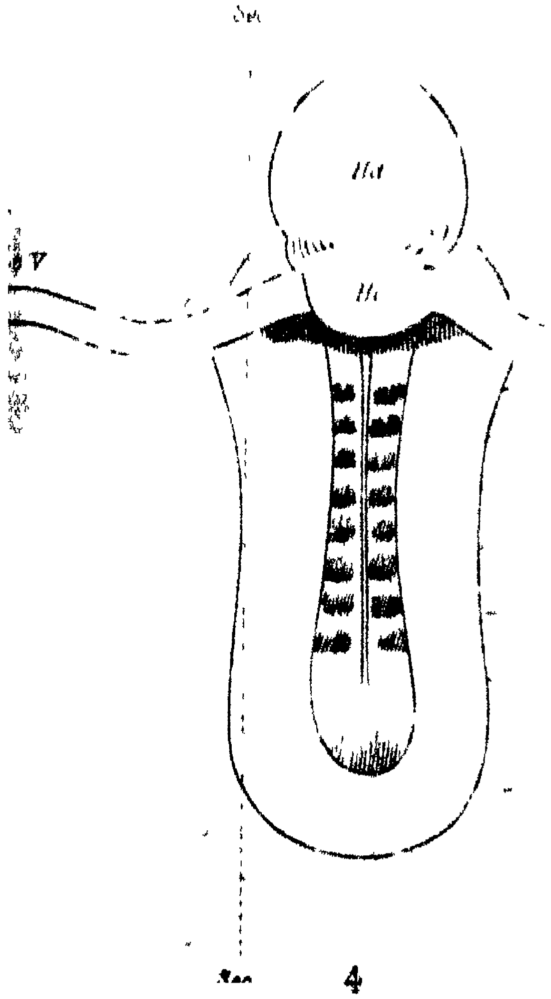
1


Hl
V
Hv
Ht
Ao
Ao

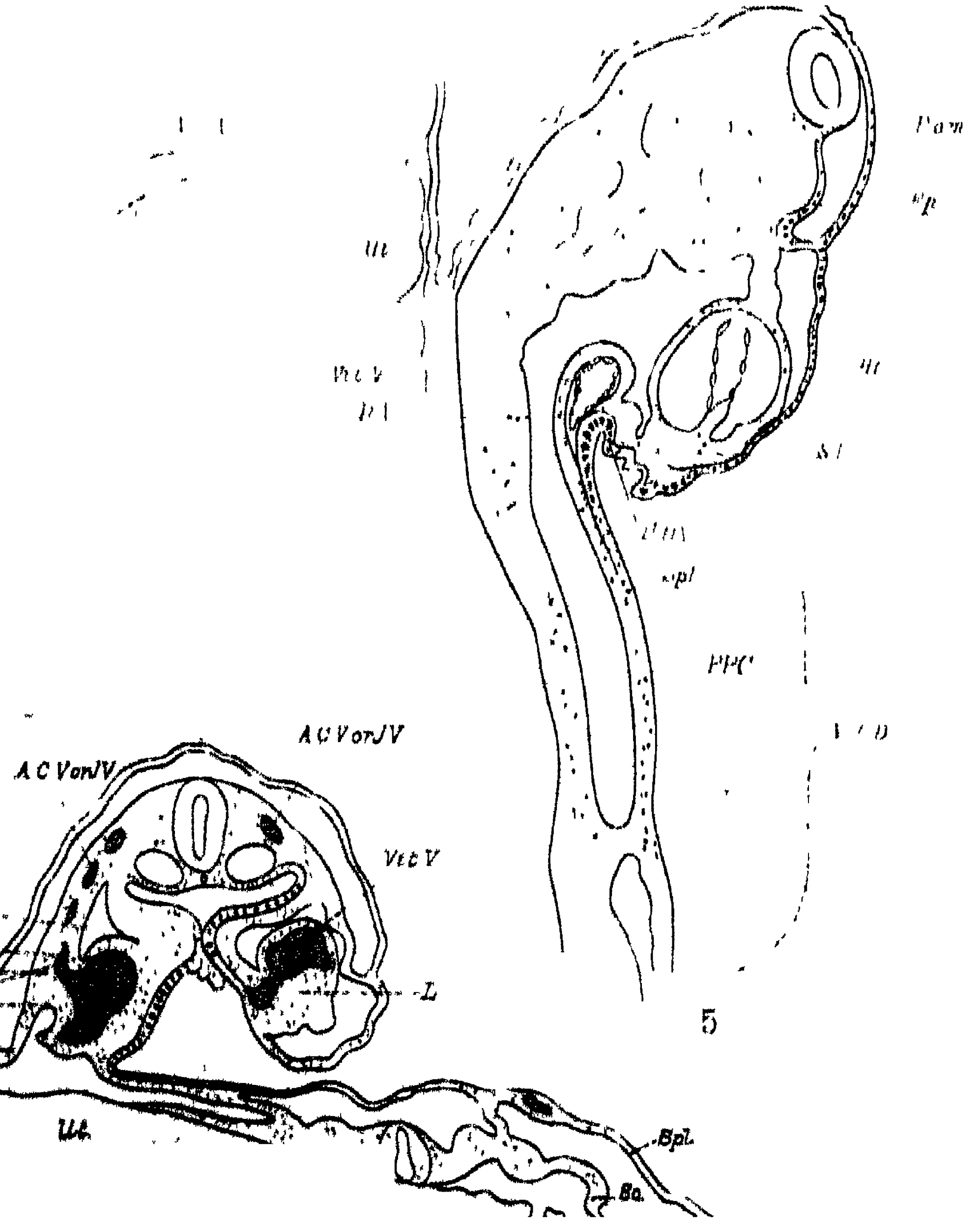
2


Pp
Hv
Ap
Spl

3


Sec
Ht
Ht
V
Sec

4


Pam
Ep
Ht
Vit V
PA
Ht
St
Spl
PPC
A C VorJV
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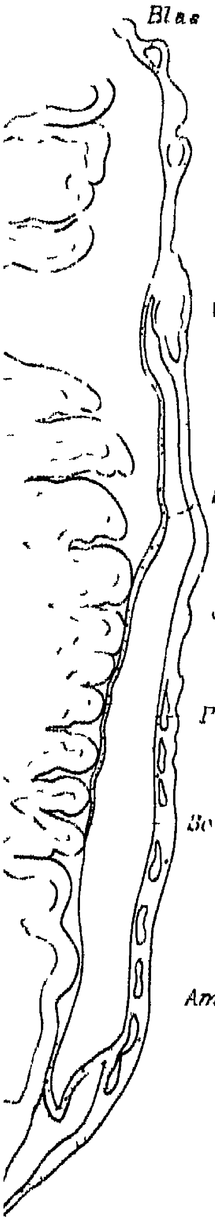
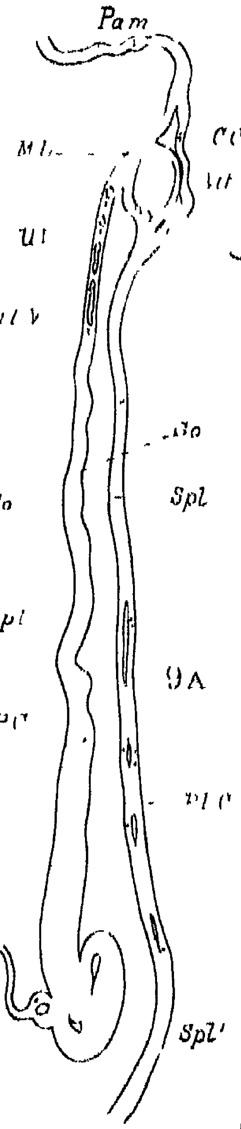
Vit V
Jt V
U.V.
S.R.
M.L.
L
Ut.
Spl.
So.

5





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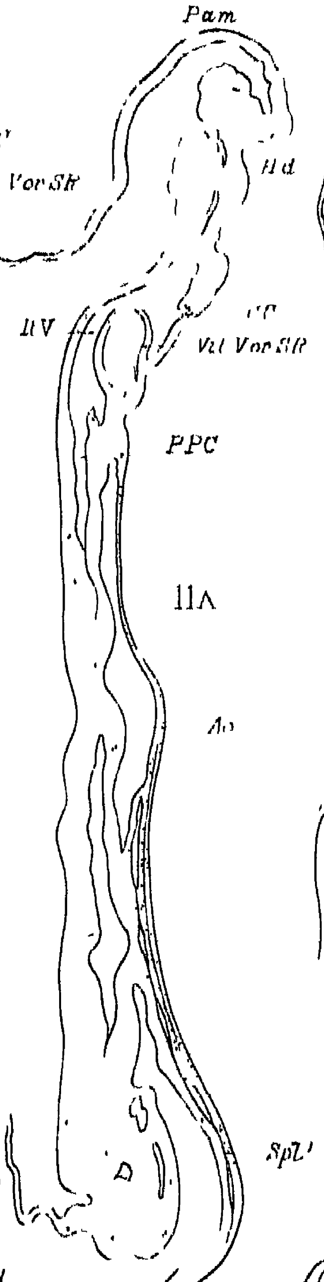

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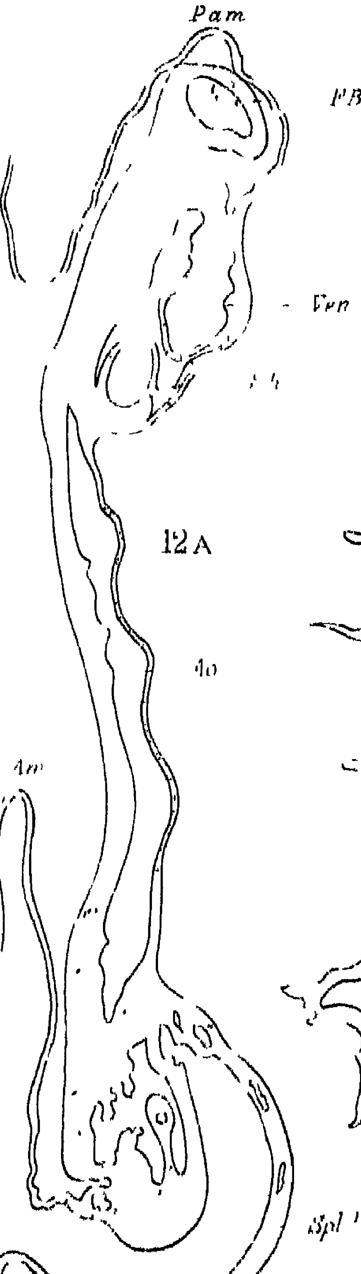

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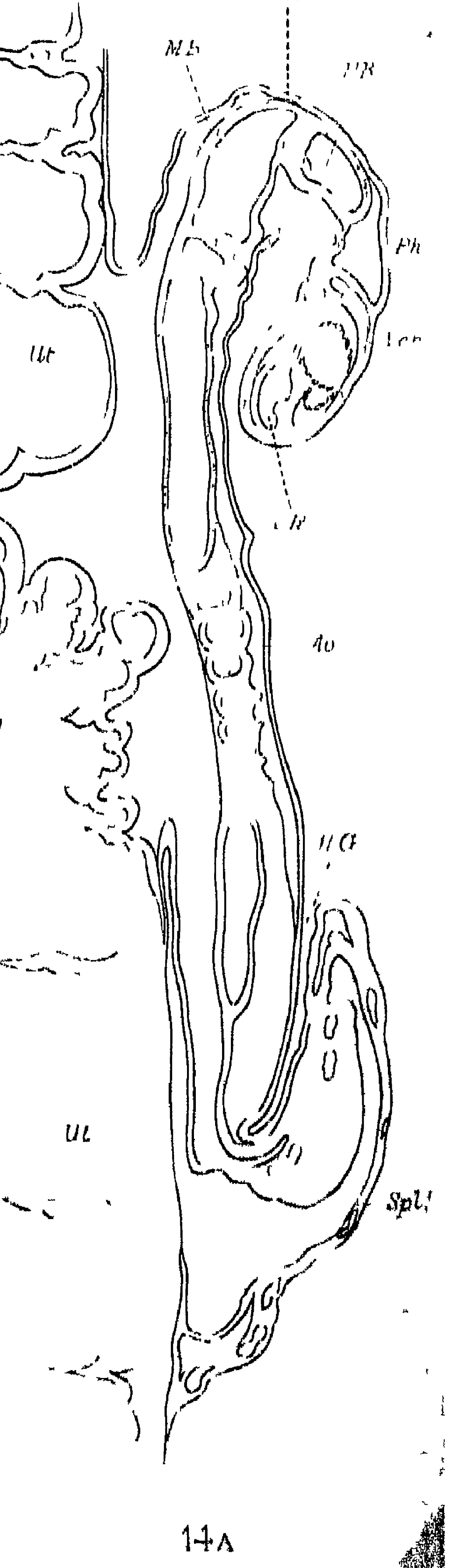

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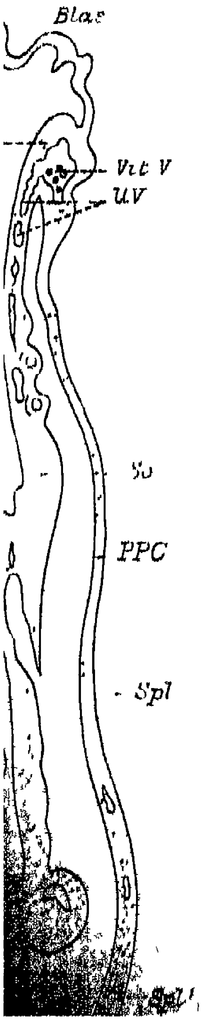

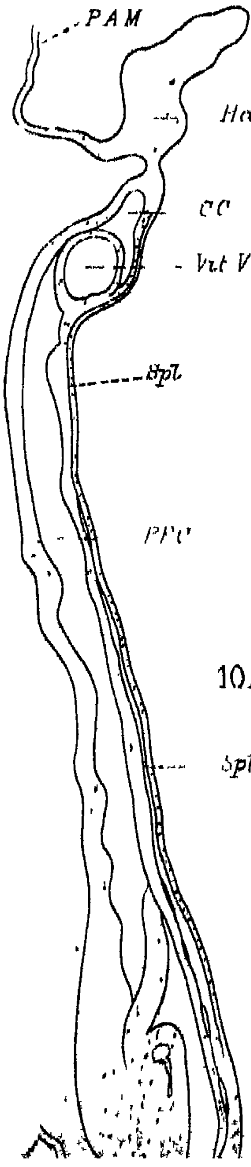

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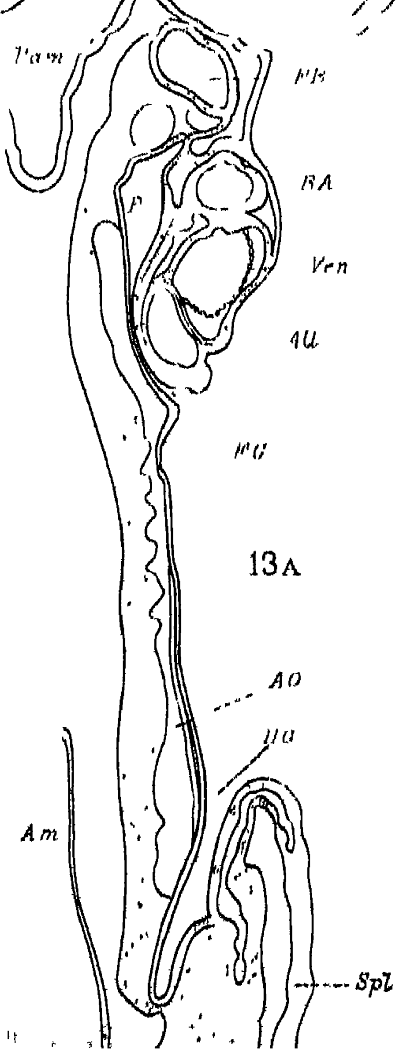

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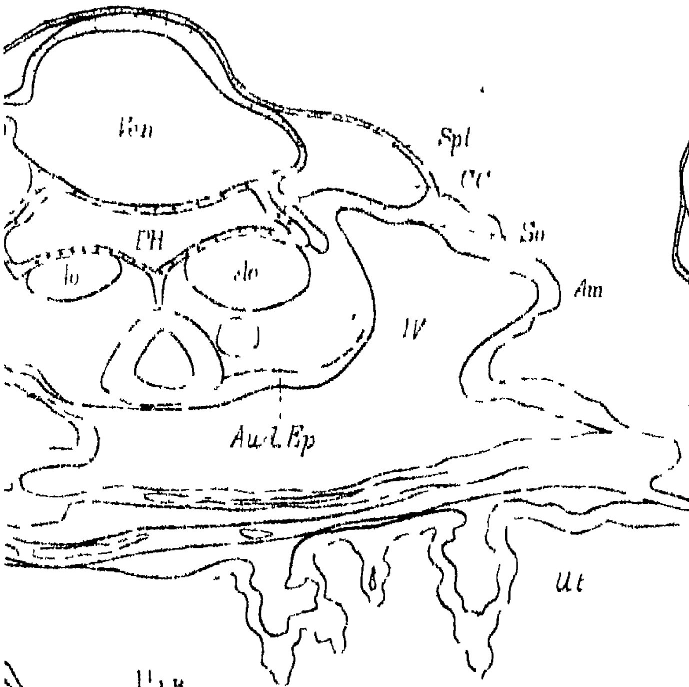

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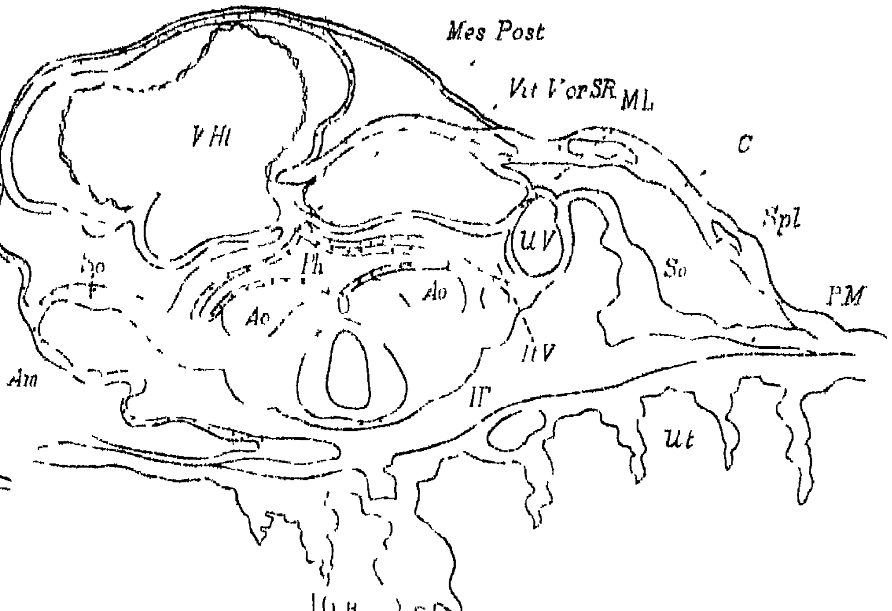

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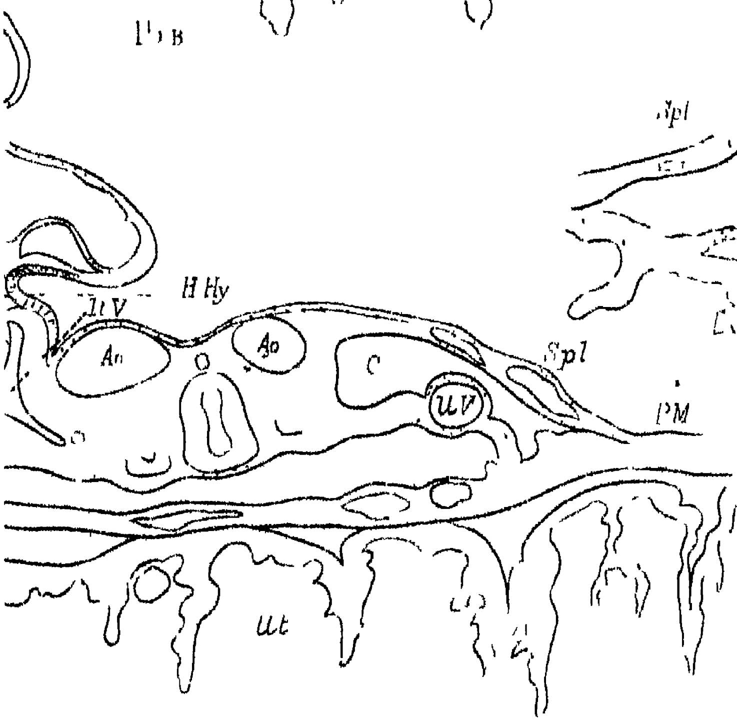

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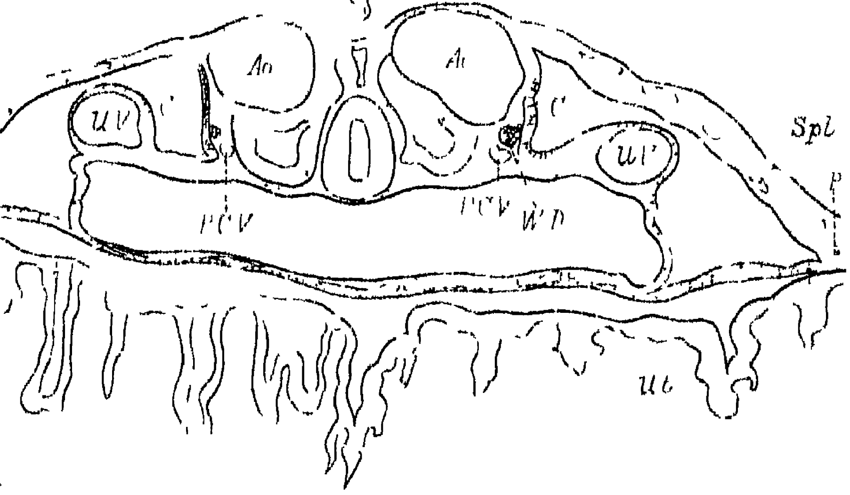

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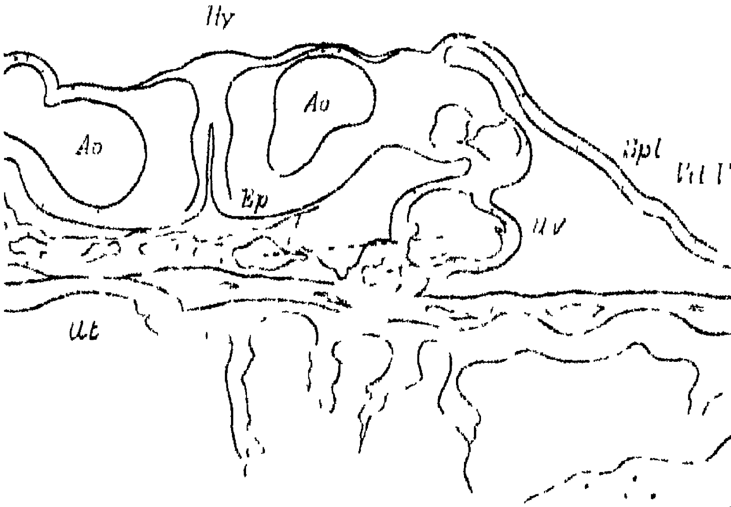

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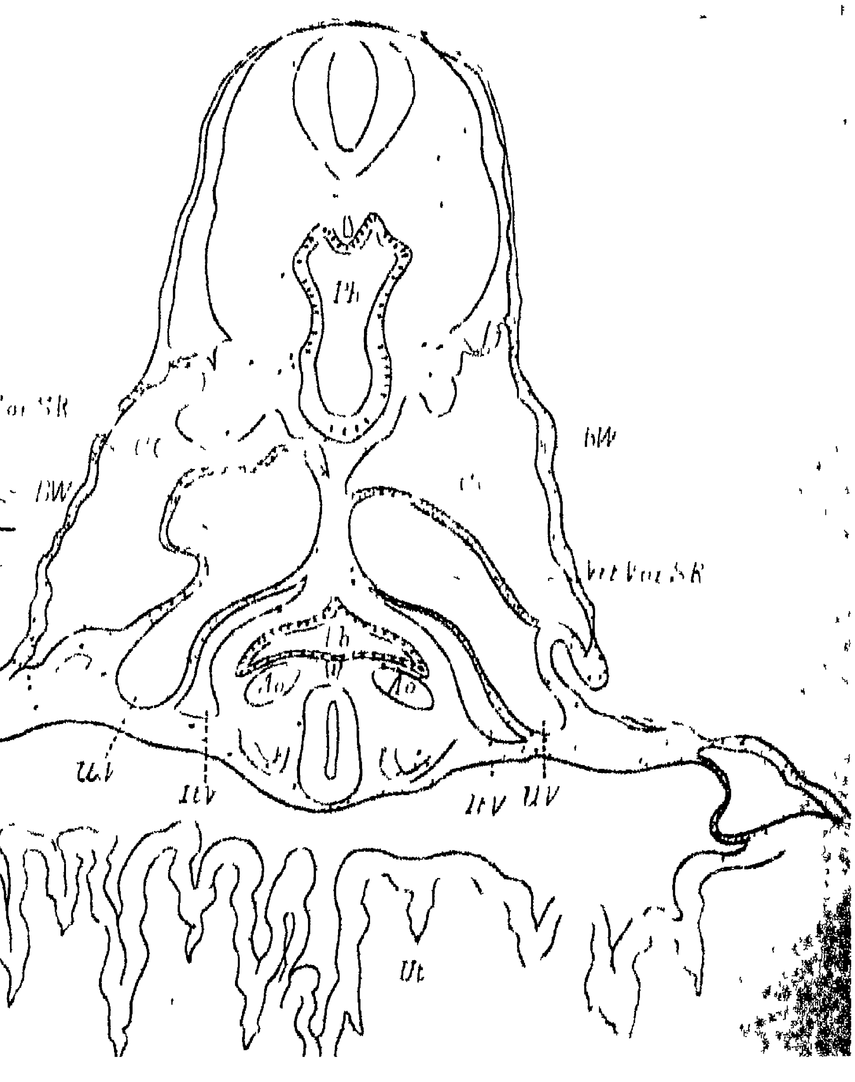

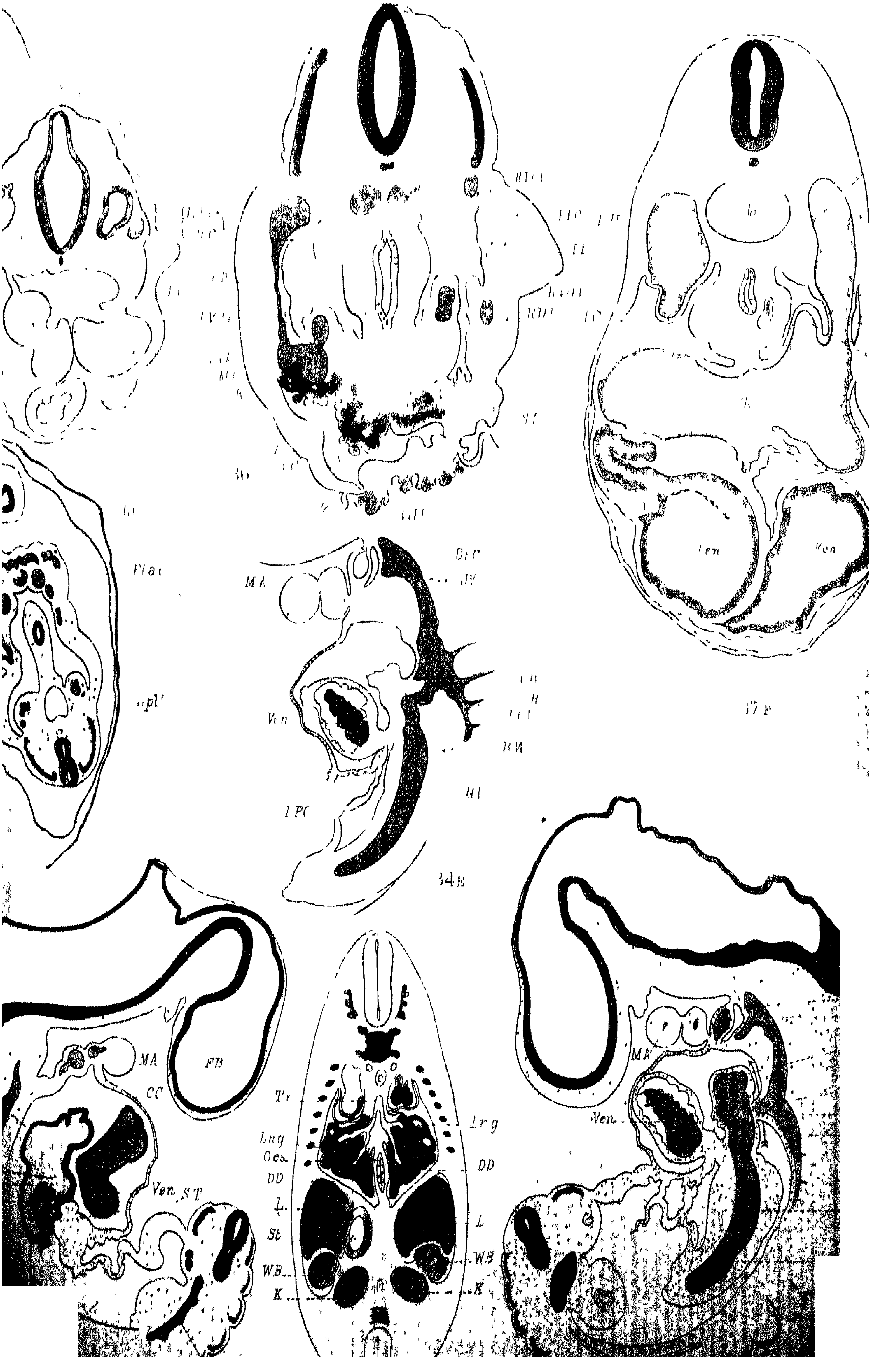
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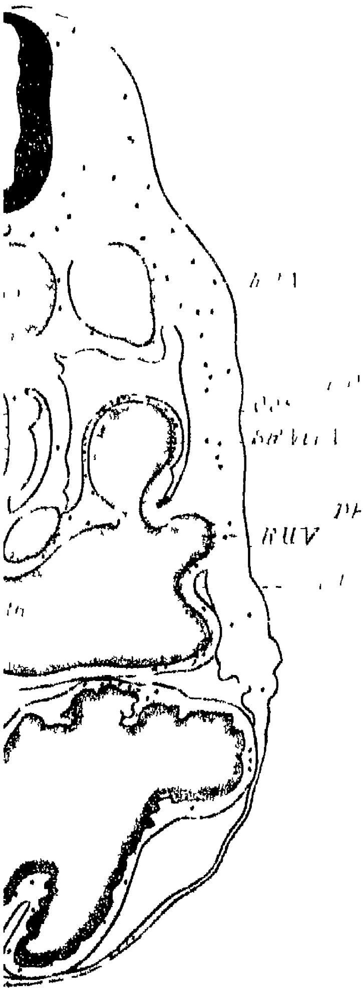

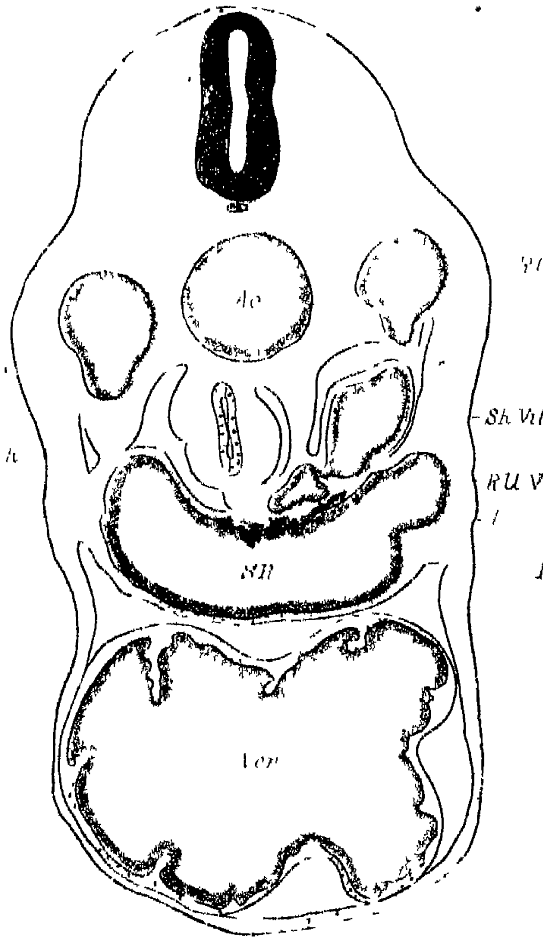

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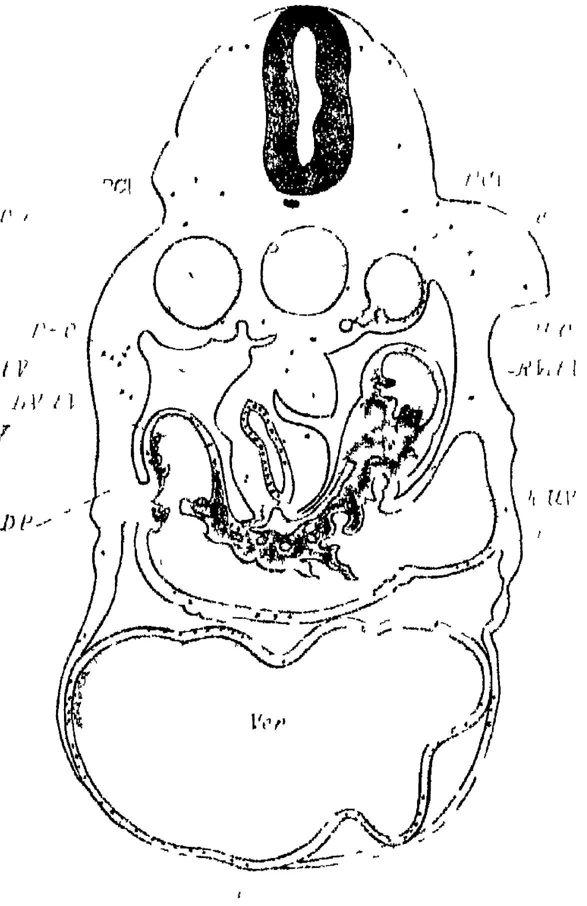

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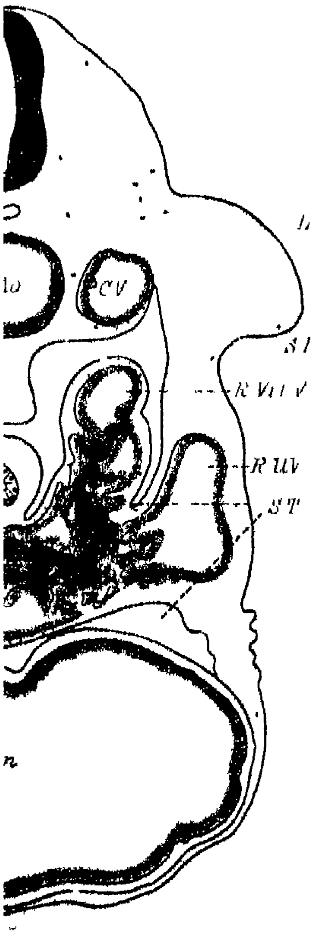

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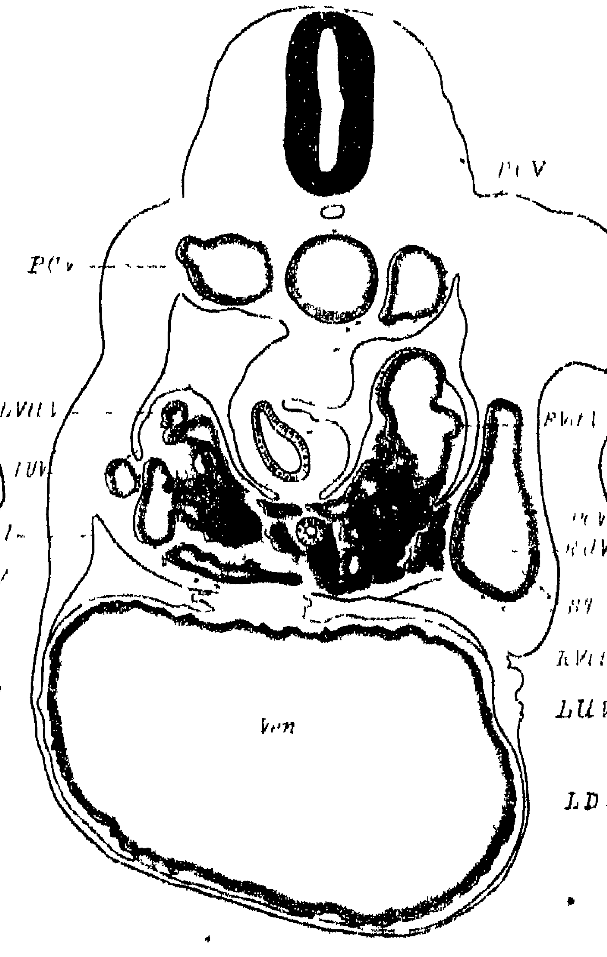

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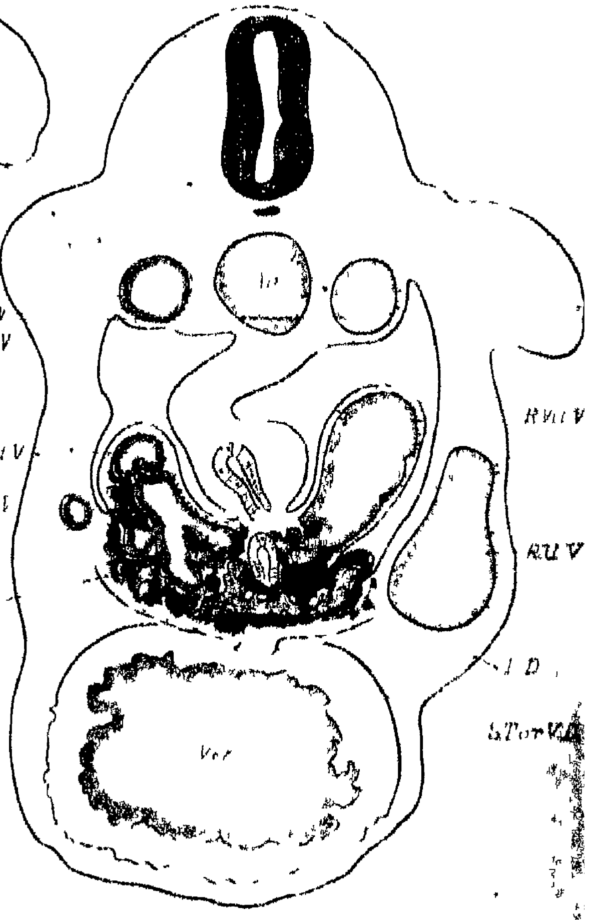

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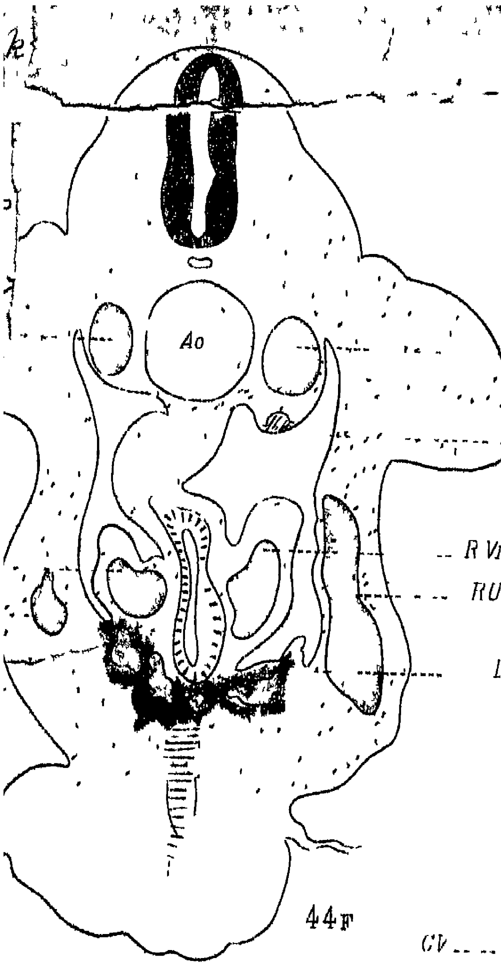

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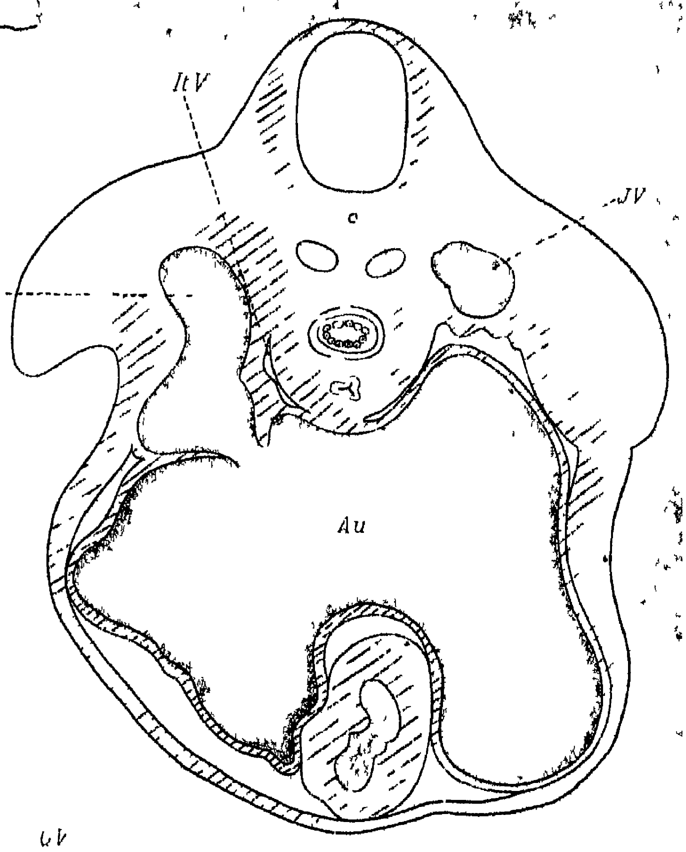

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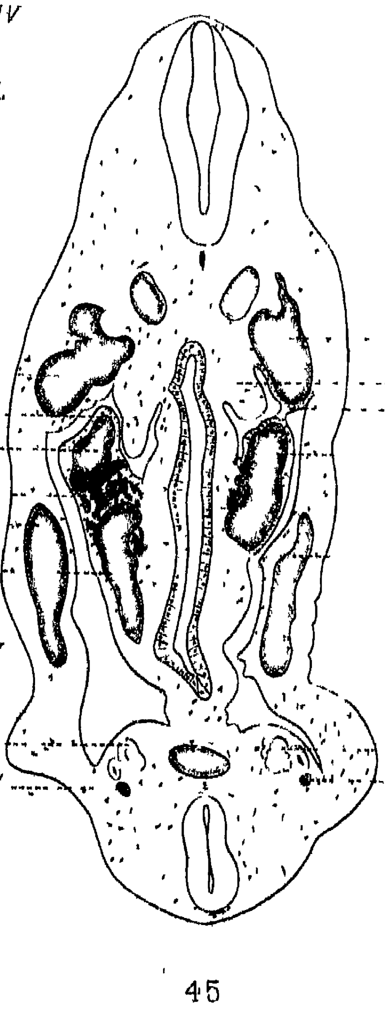

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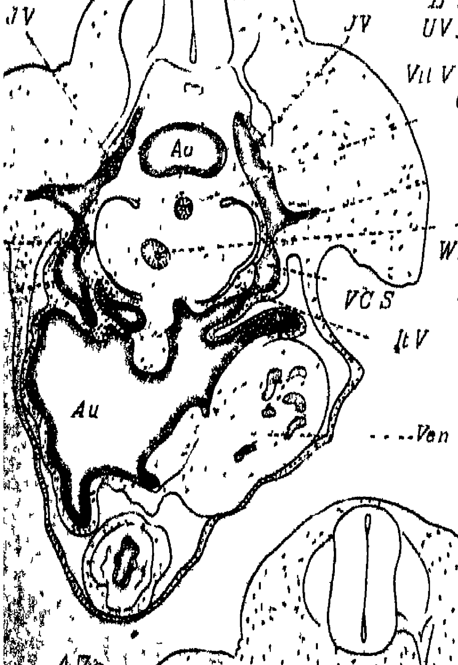

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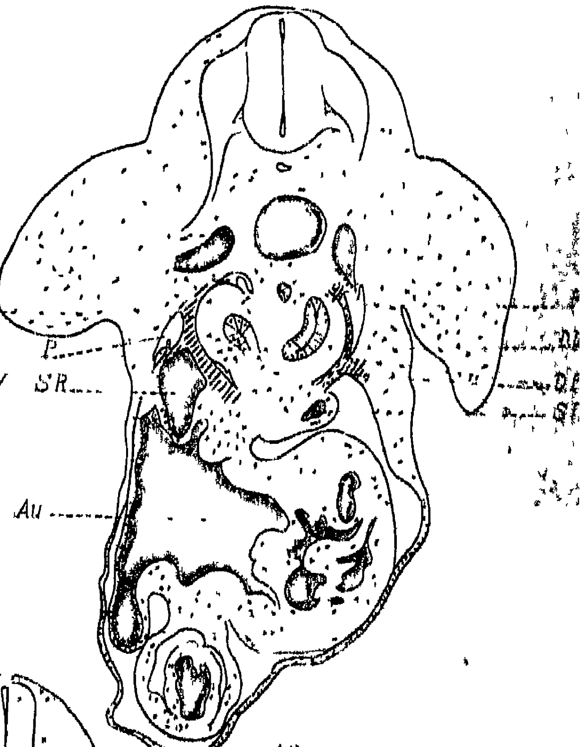
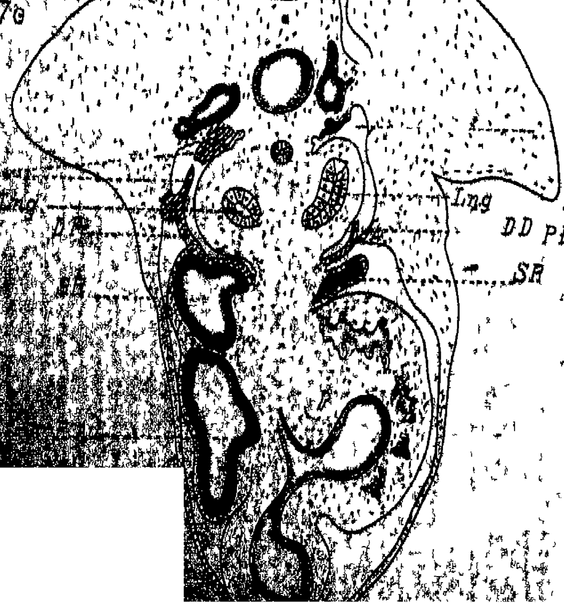
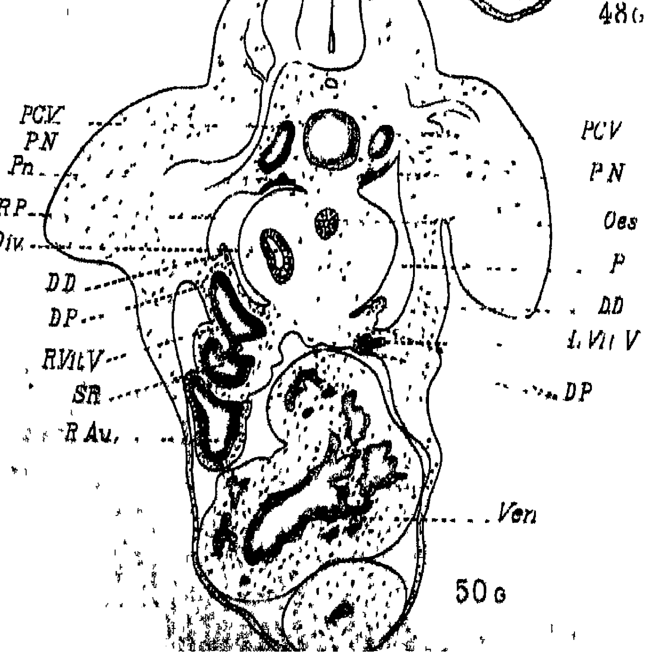


48G





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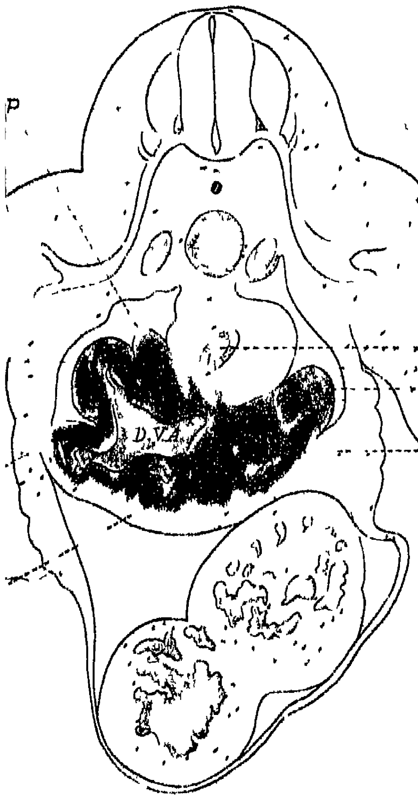
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P
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DVA

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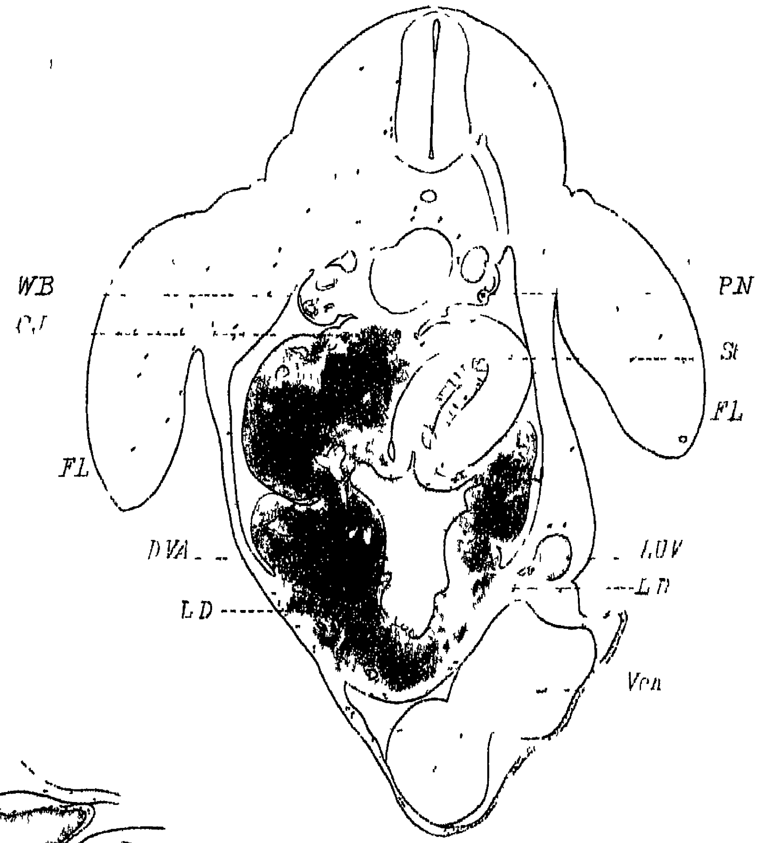
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LUV
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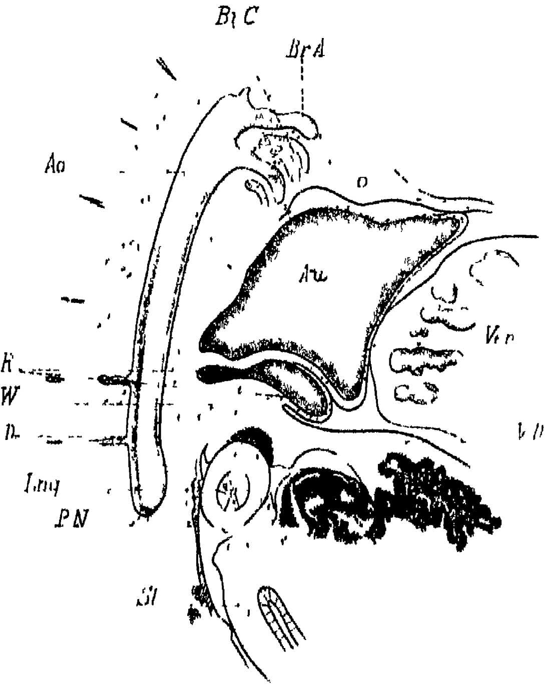
Ven

52 G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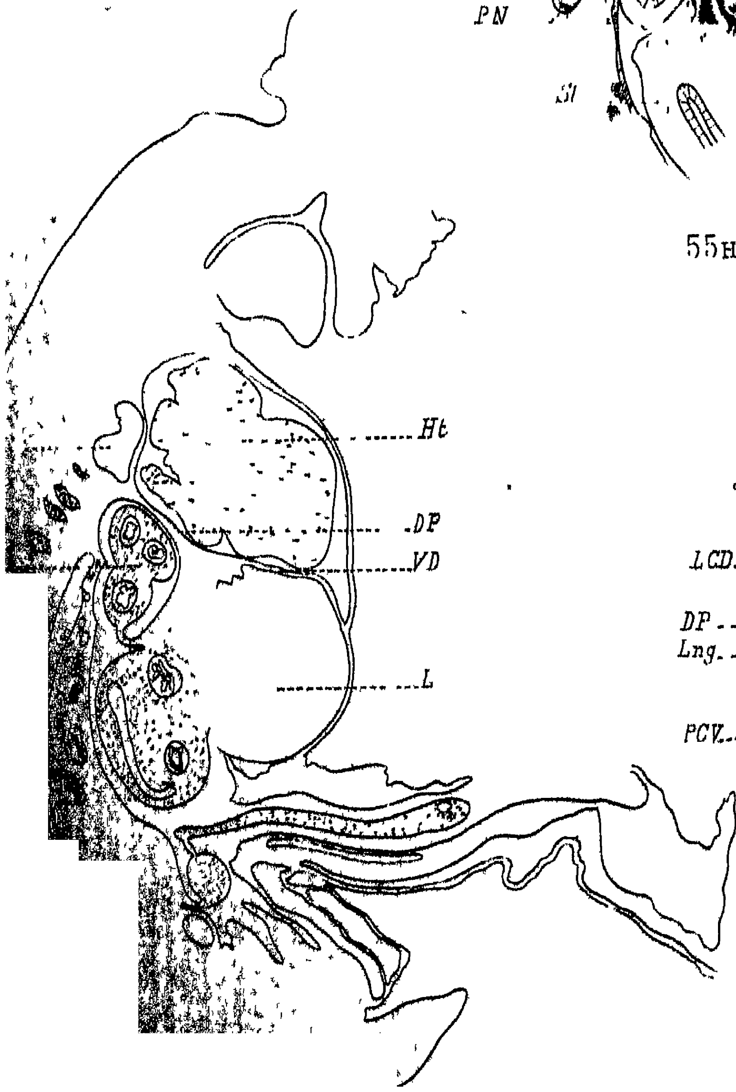
55 H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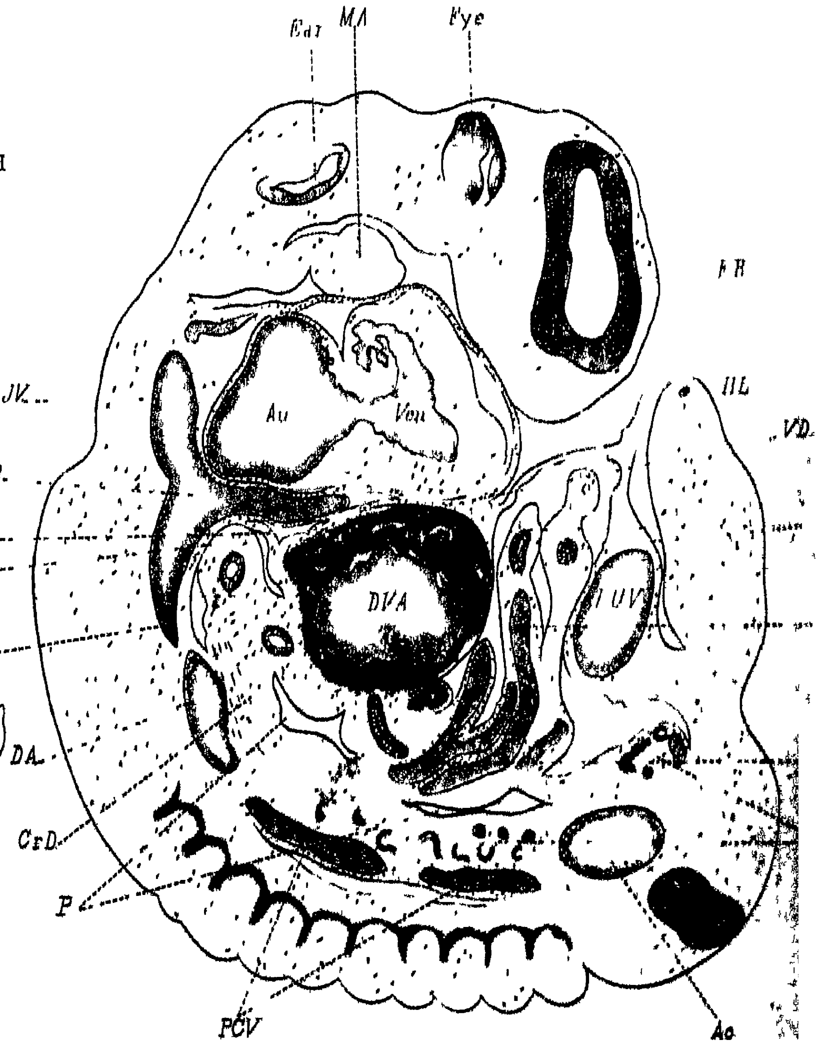
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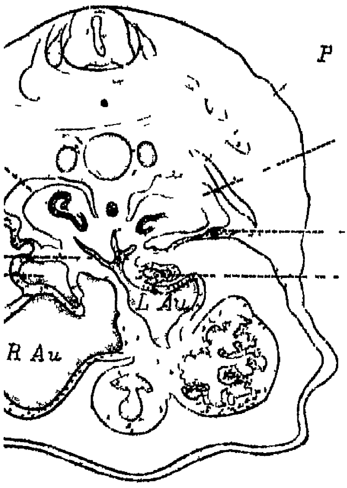

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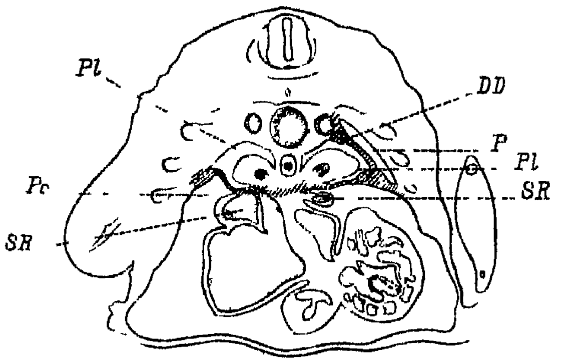

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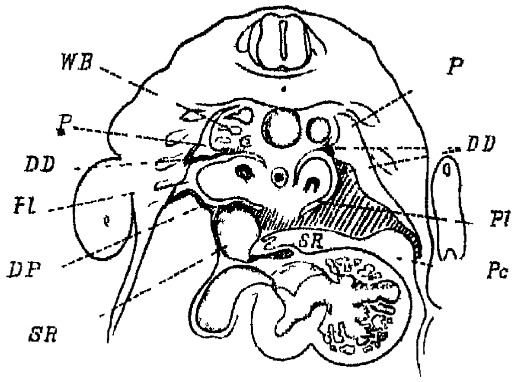

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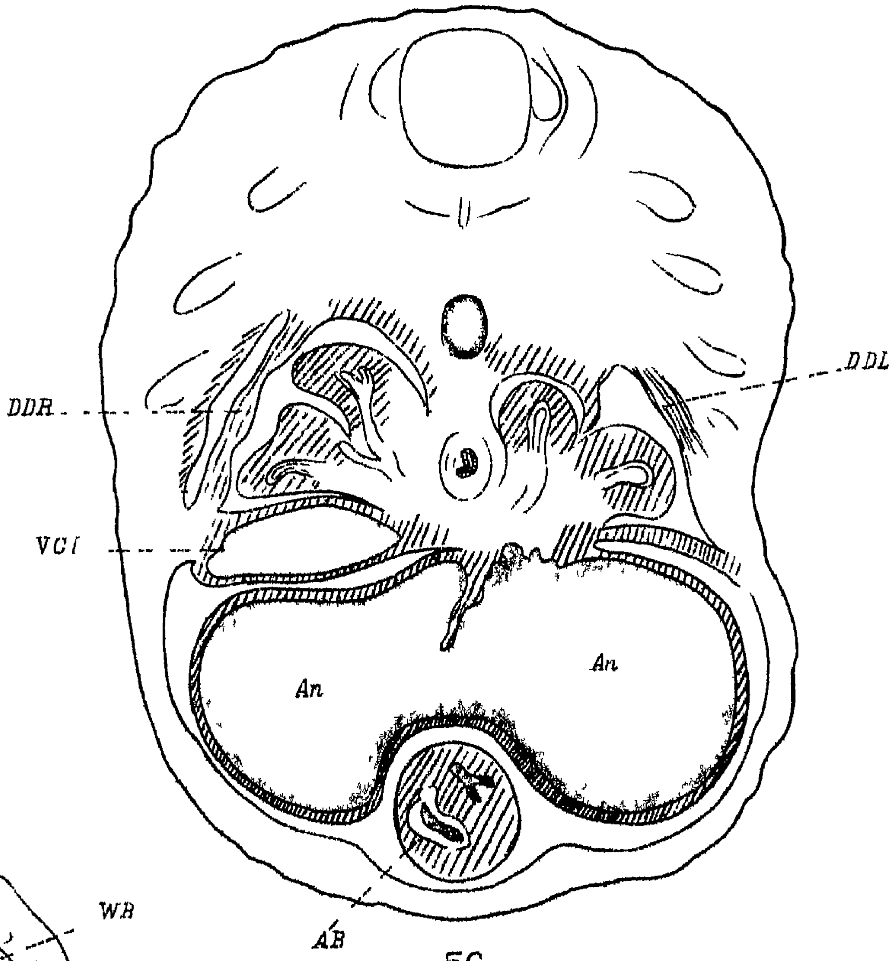

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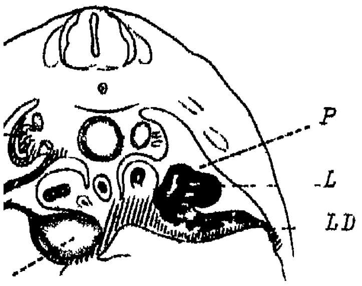

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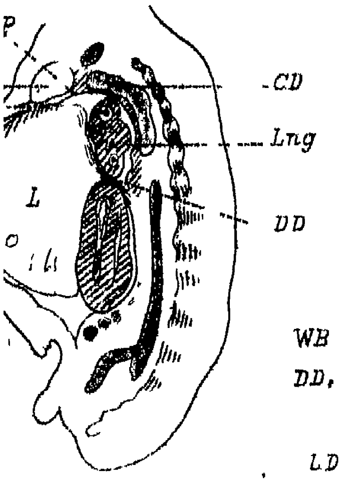

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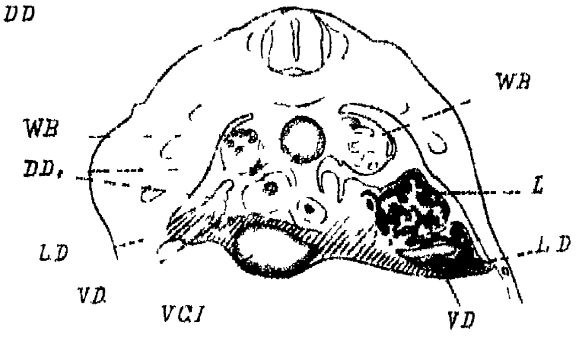

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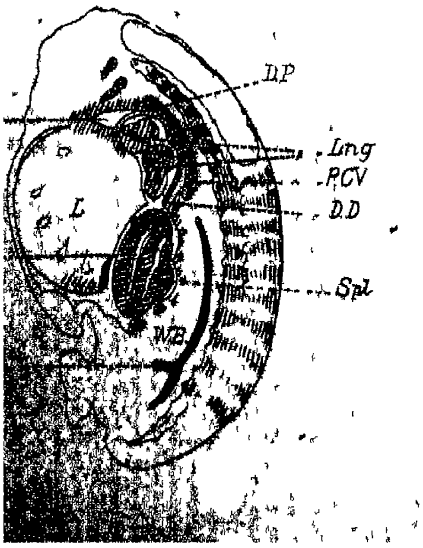

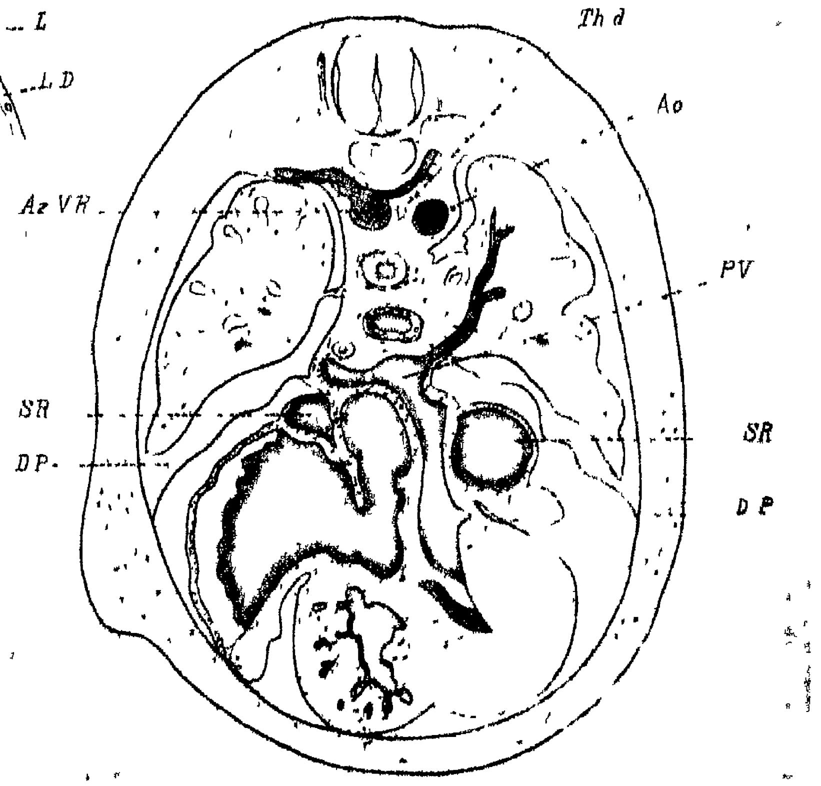

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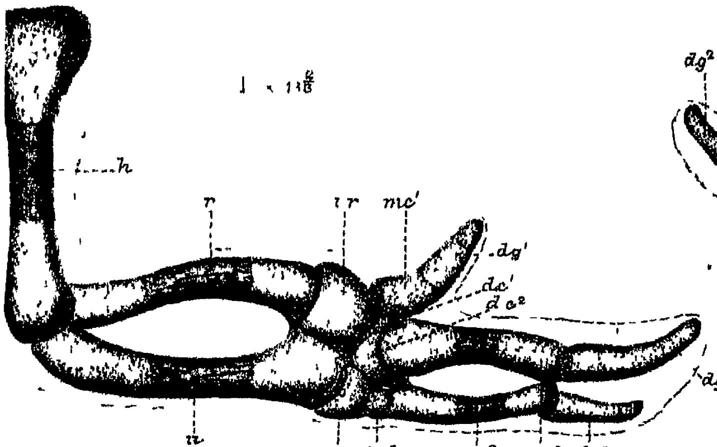

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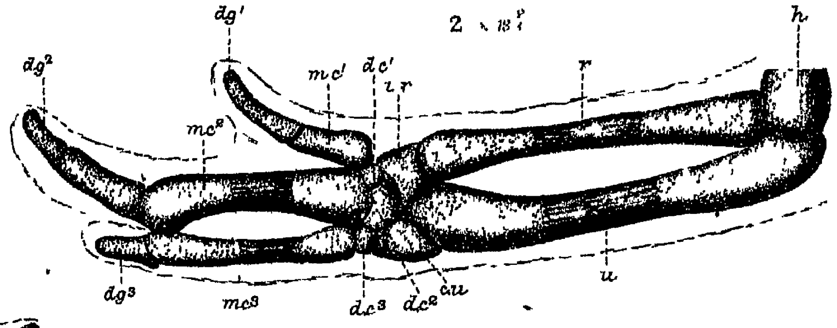

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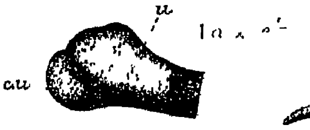

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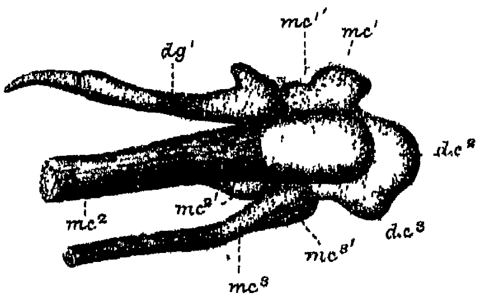

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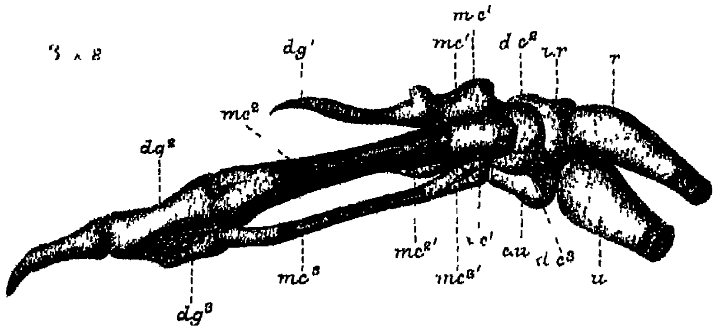

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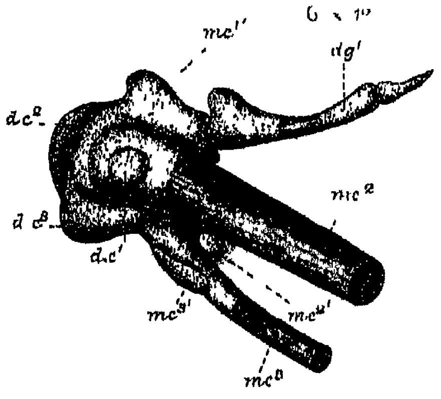

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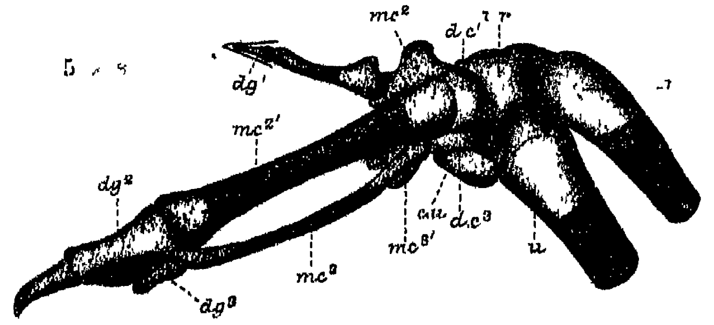

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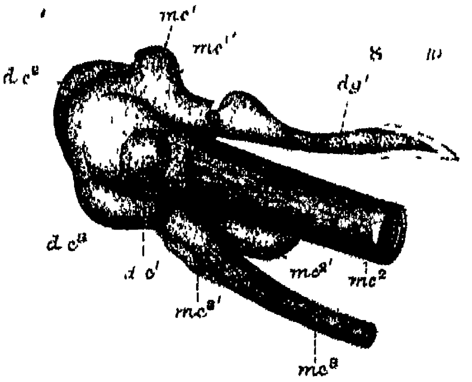

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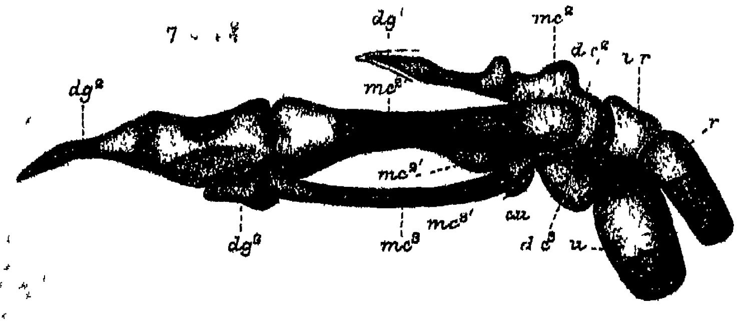

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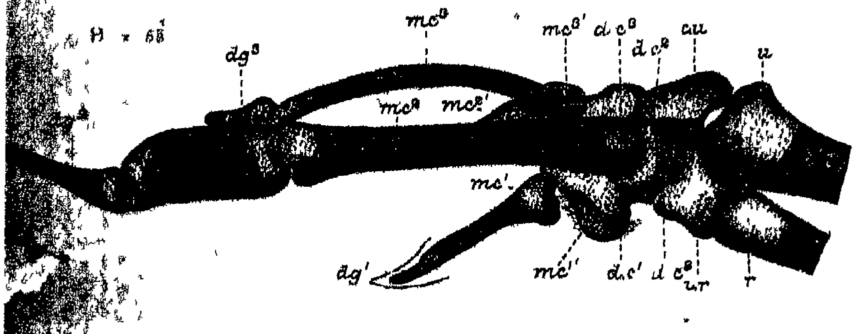

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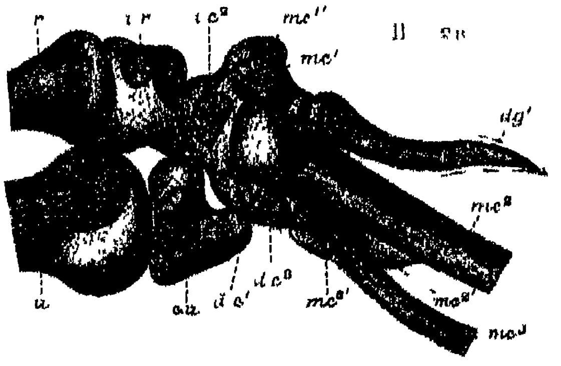

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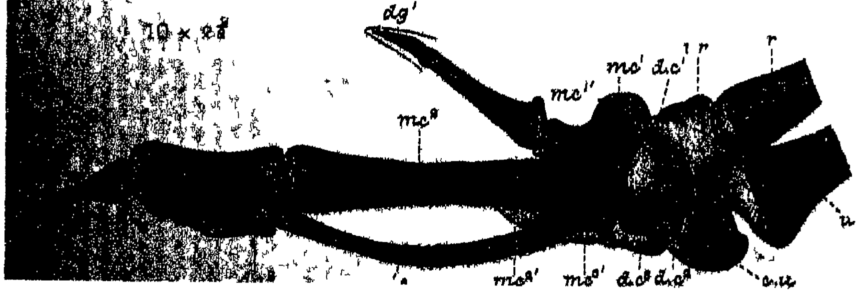

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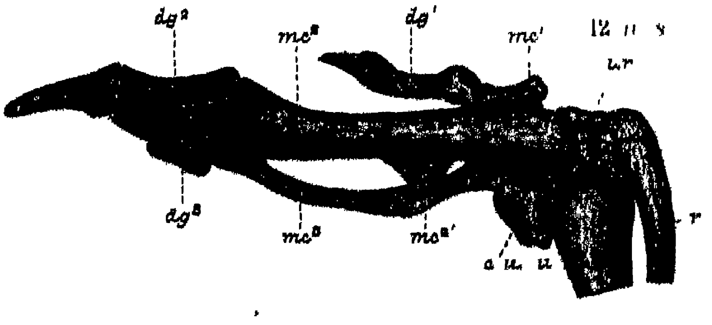

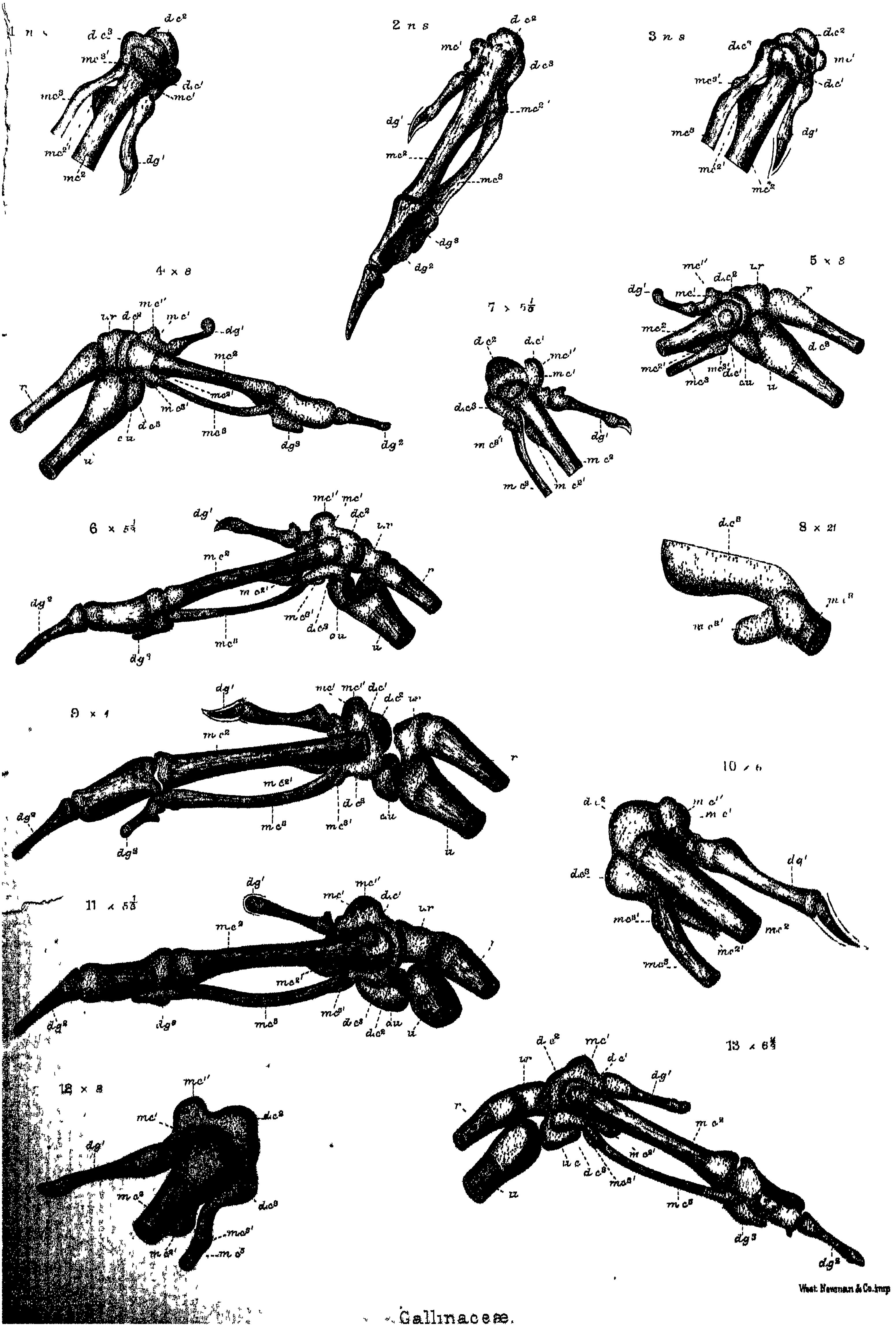

West, Newman & Co. imp.

Gallinaceæ.

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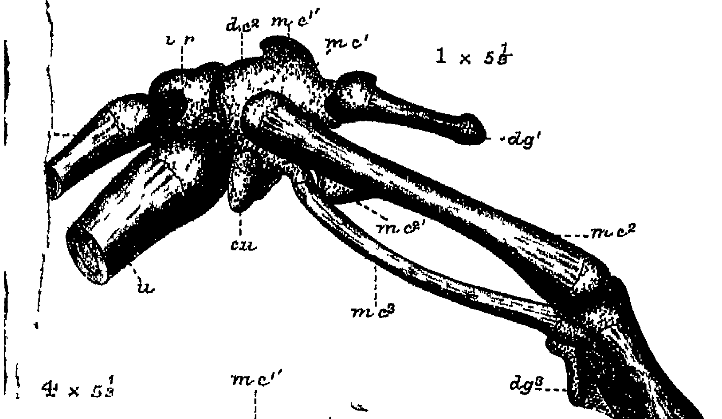

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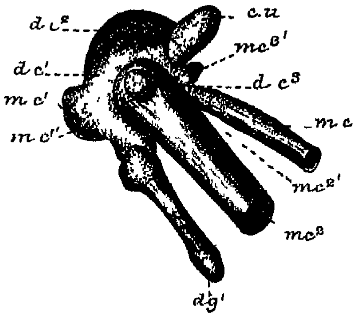

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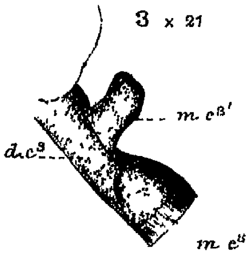

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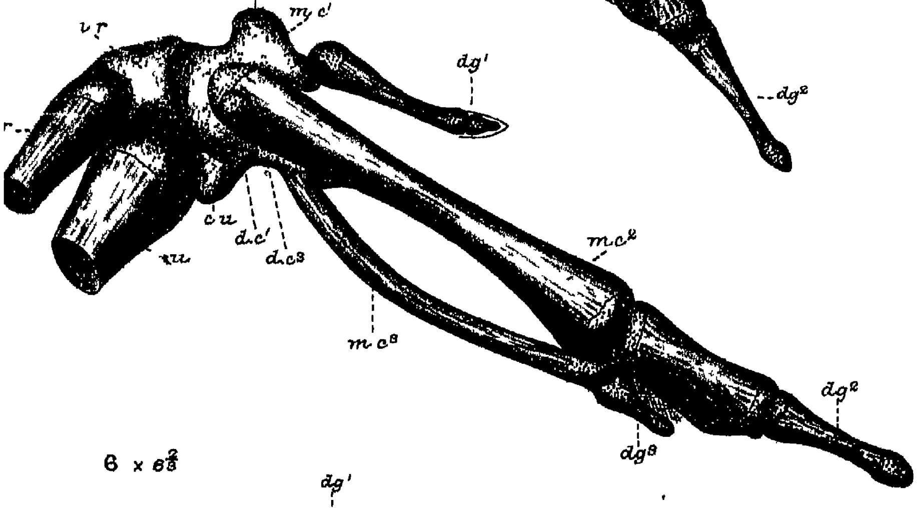

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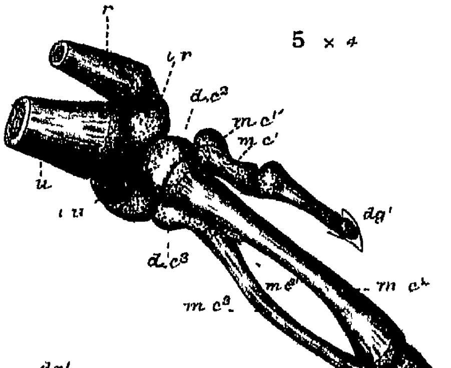

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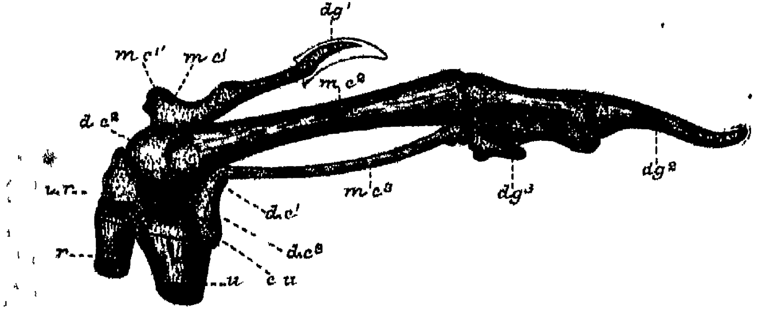

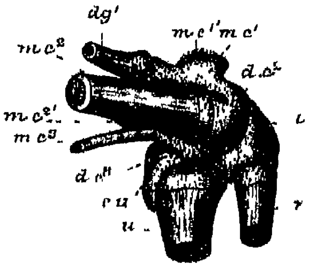

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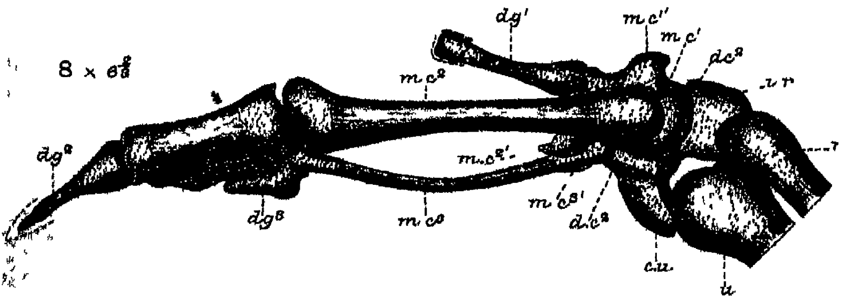
8 × 6$\frac{2}{3}$



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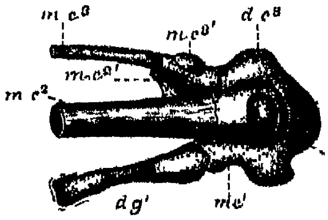

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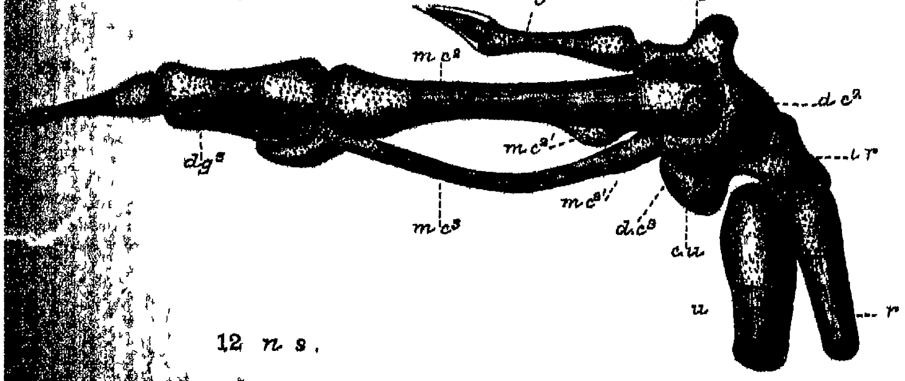

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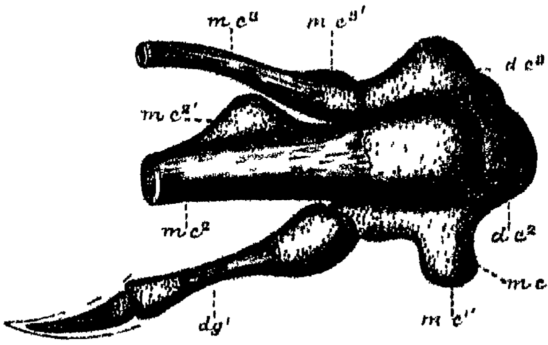
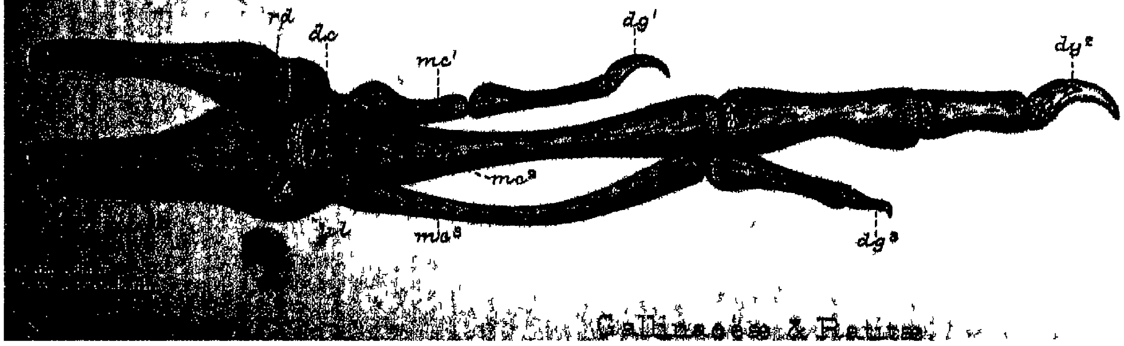


12 n. s.



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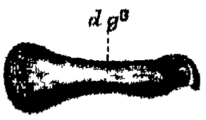
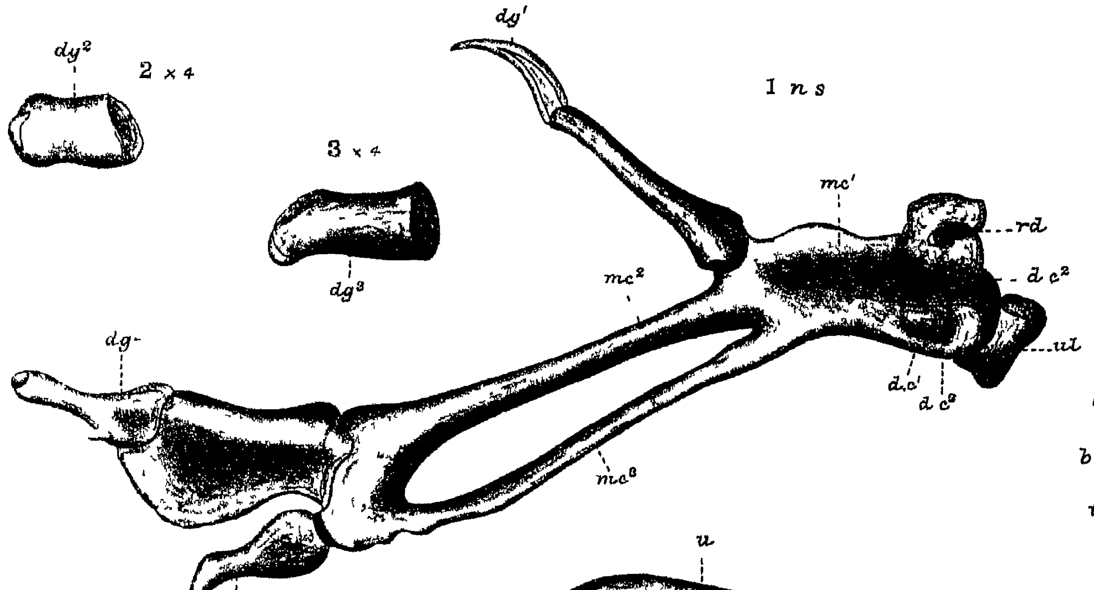


Gallinaceae & Ratitae.

West Newman & Co. imp.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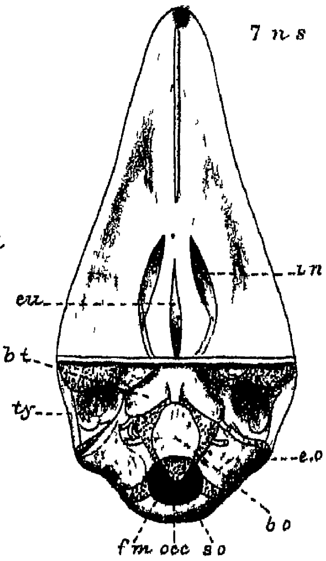
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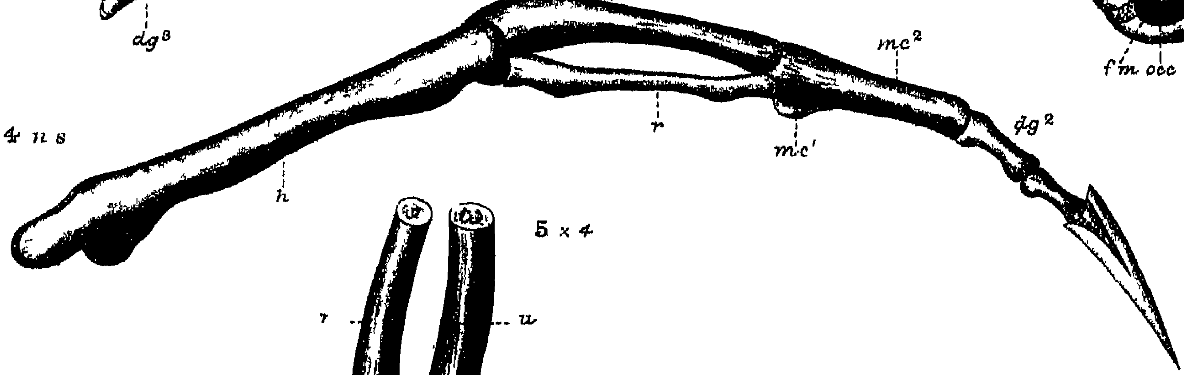
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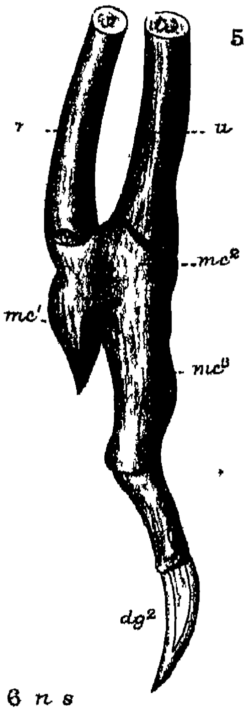
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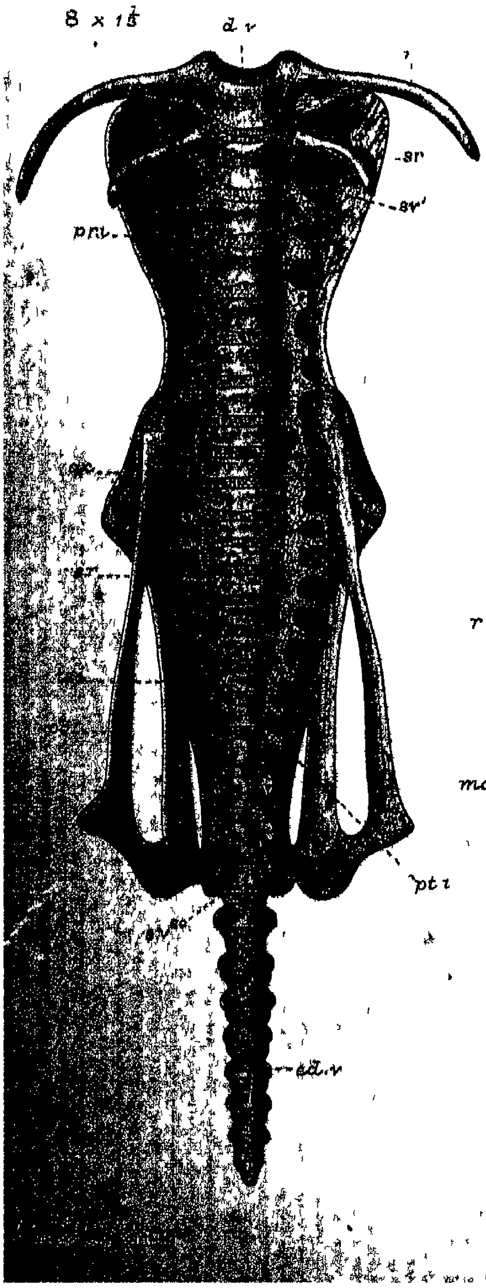
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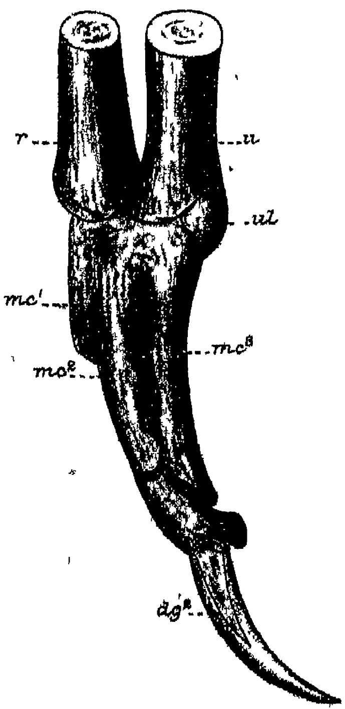
6 ns
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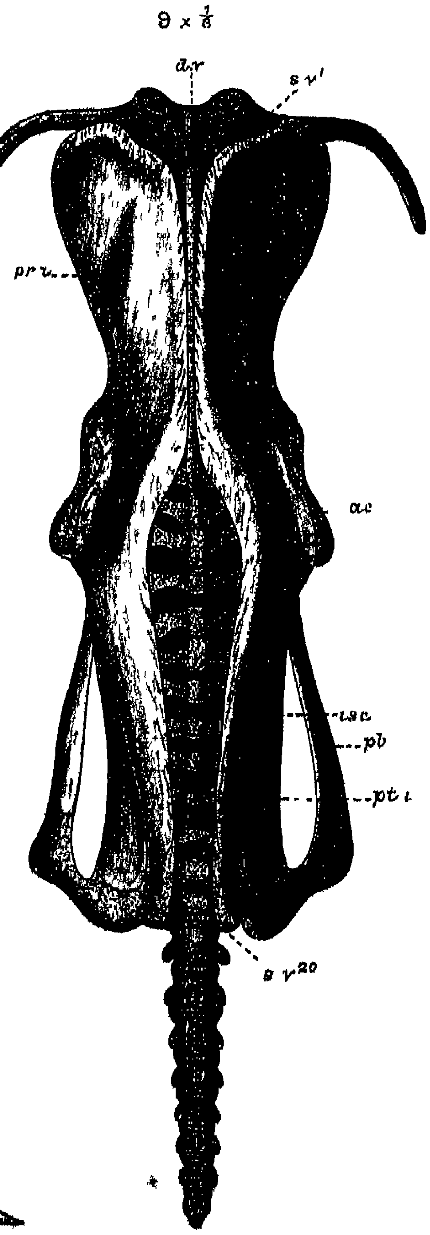
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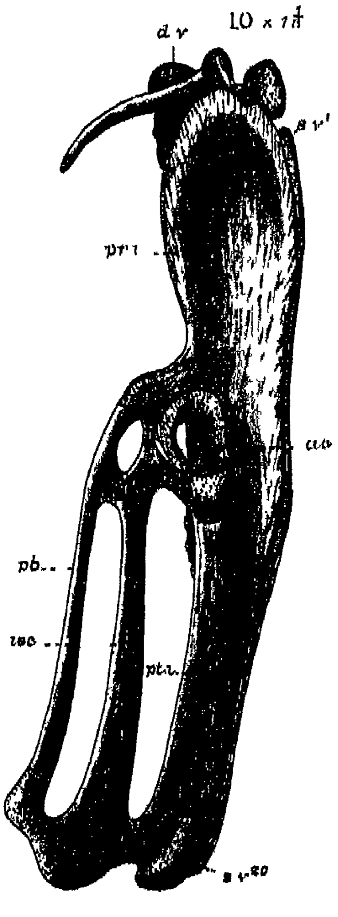
10 × 1⅓
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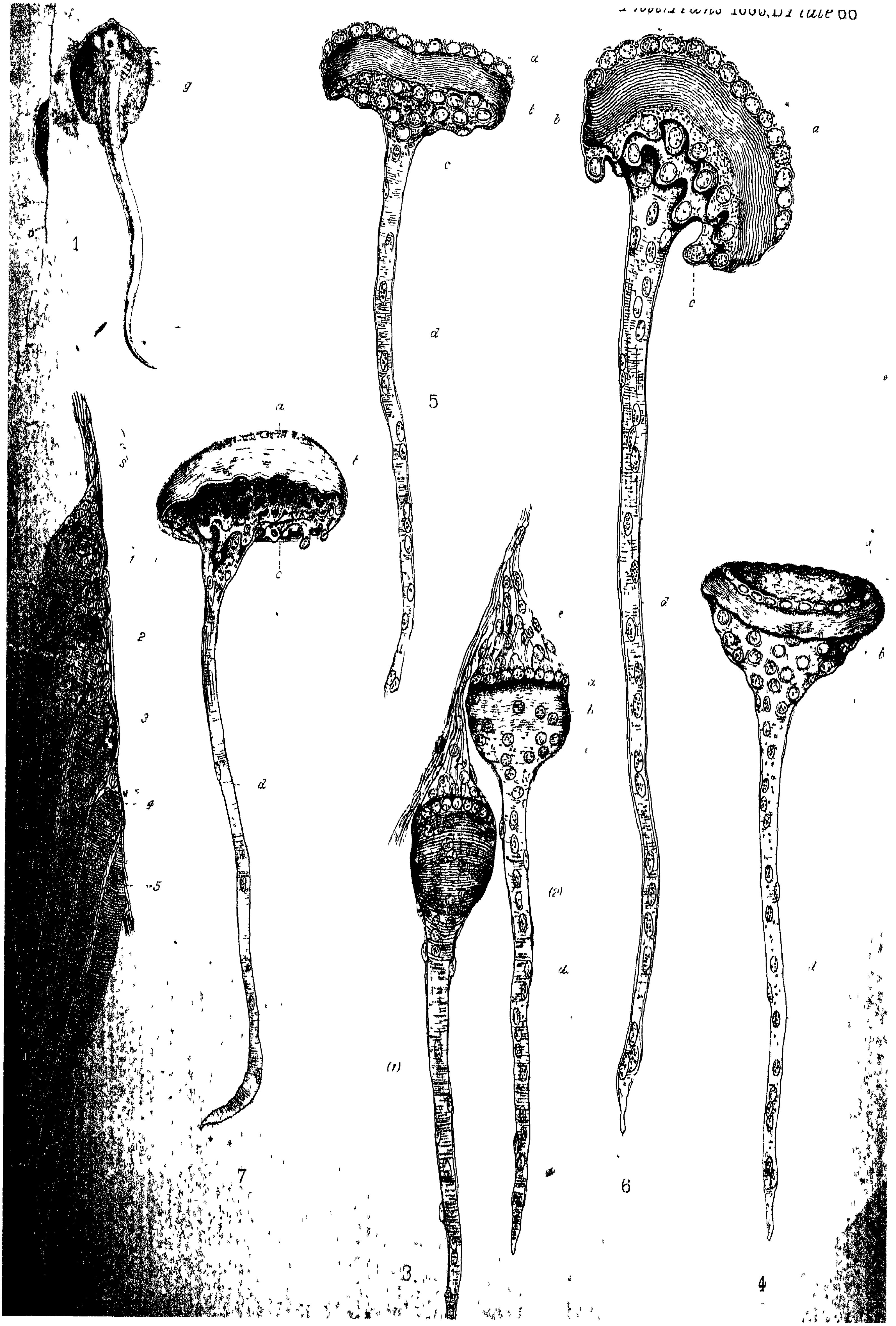
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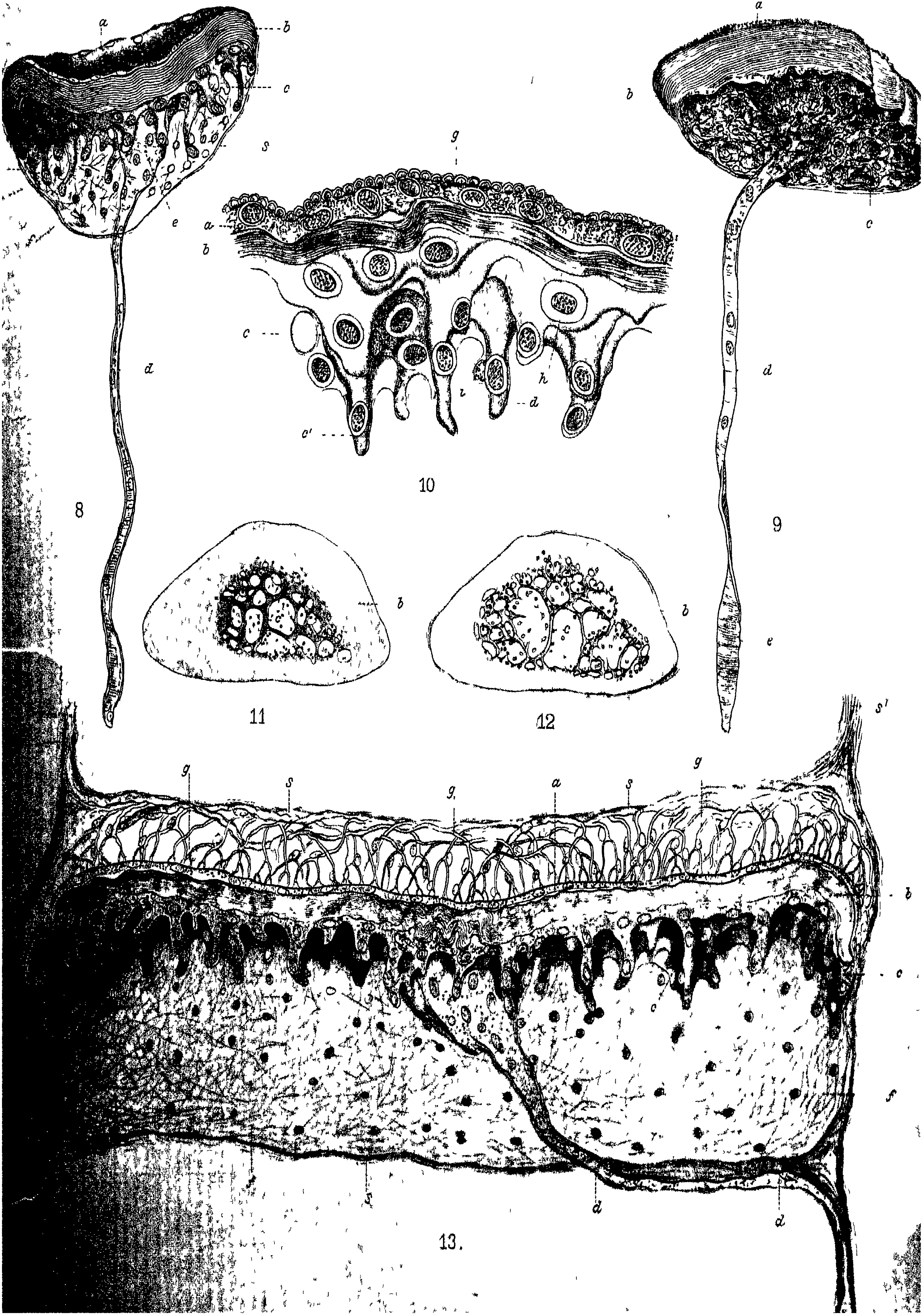

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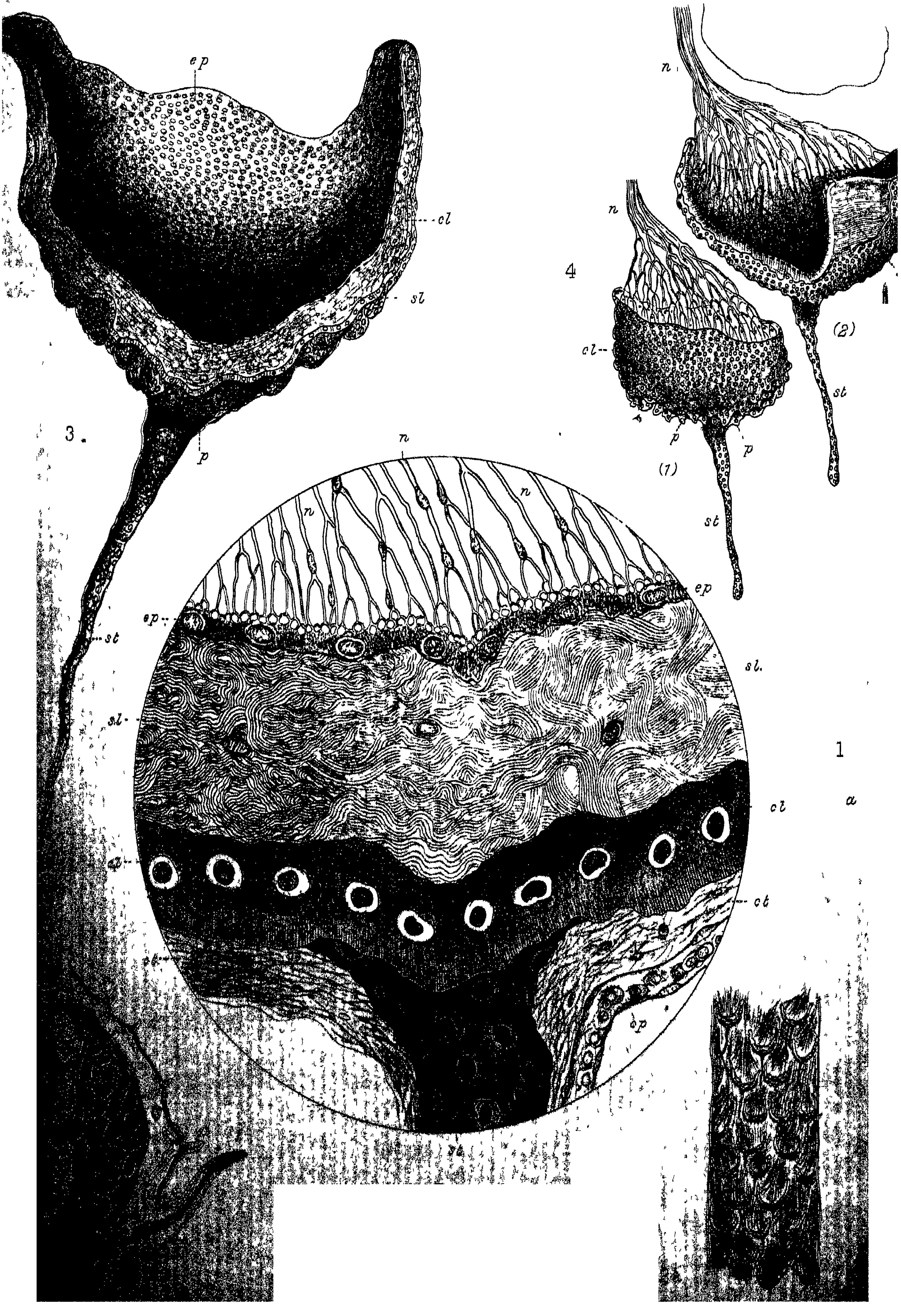

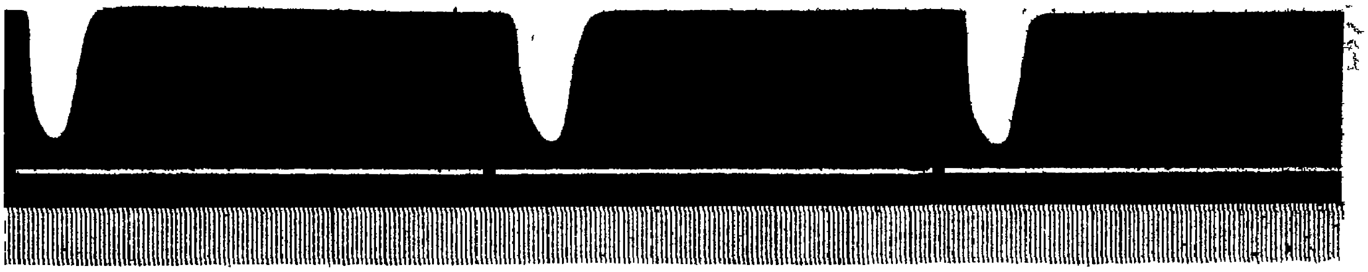

Fig 1

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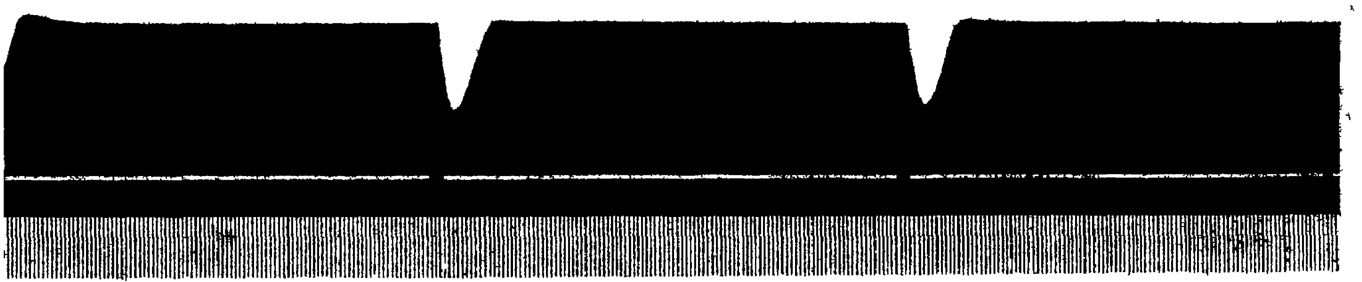

Fig 2

20 per sec

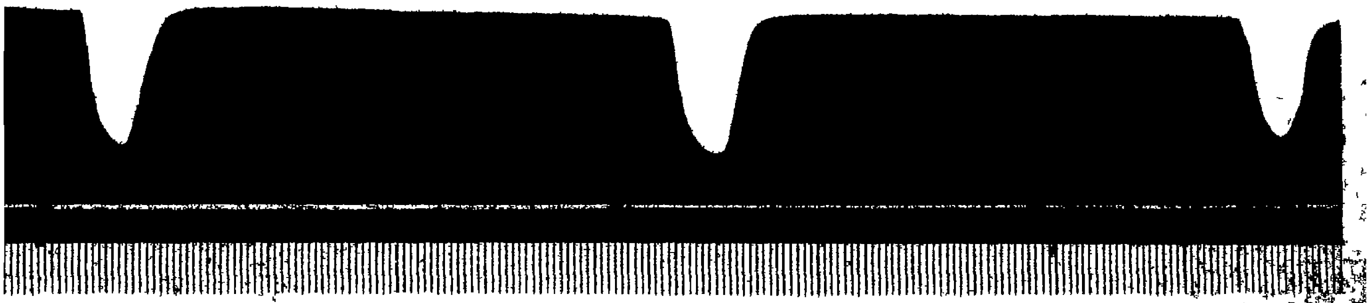

Fig. 3

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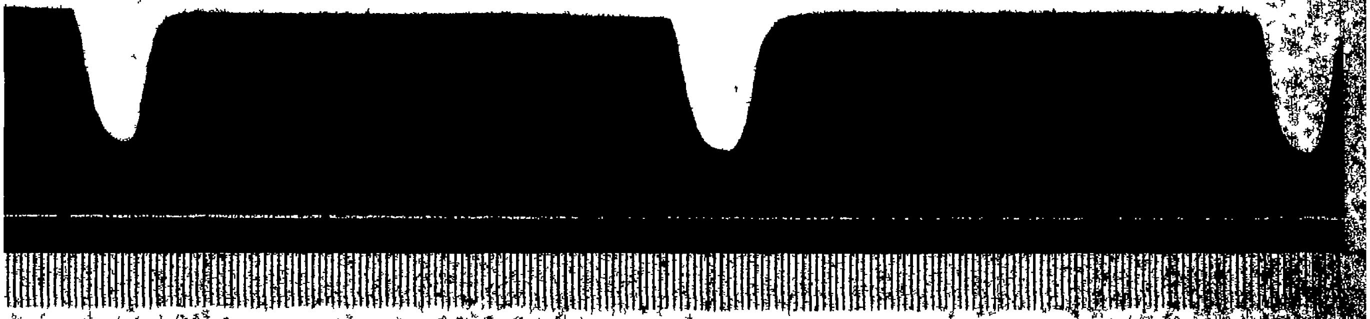
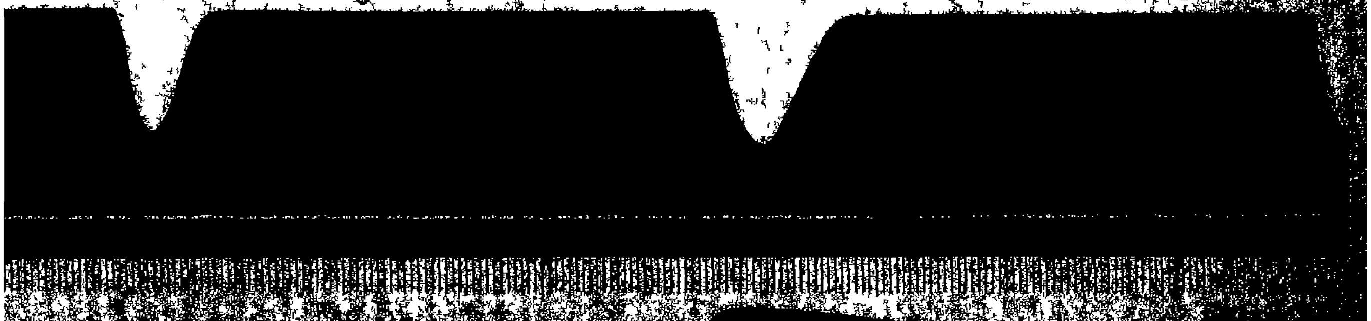
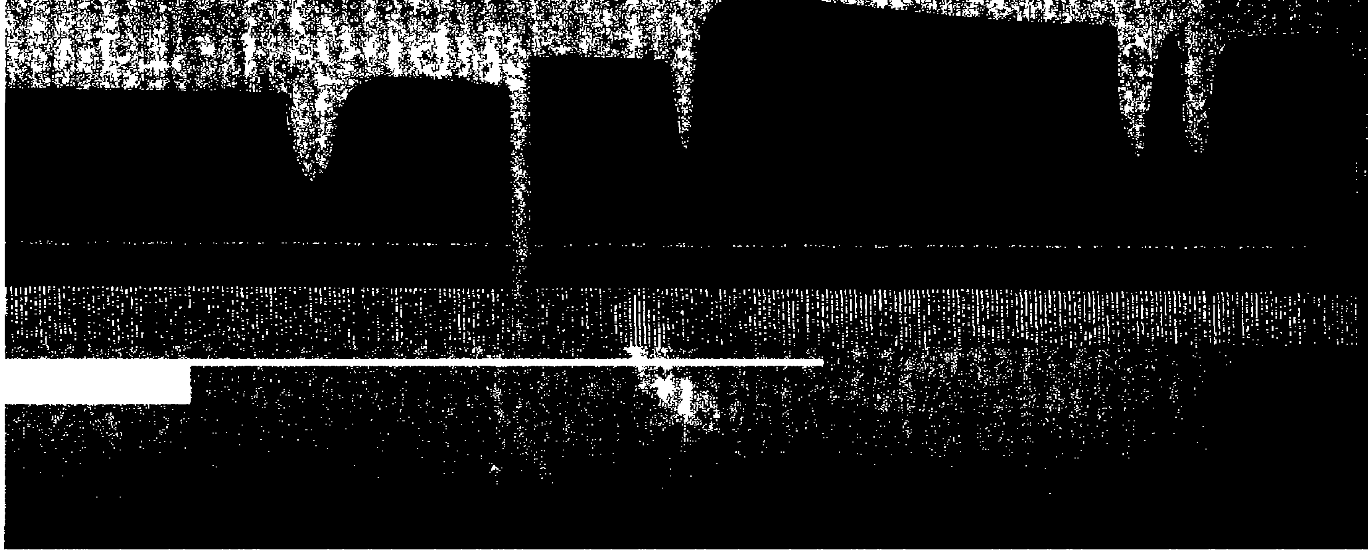


Fig 4





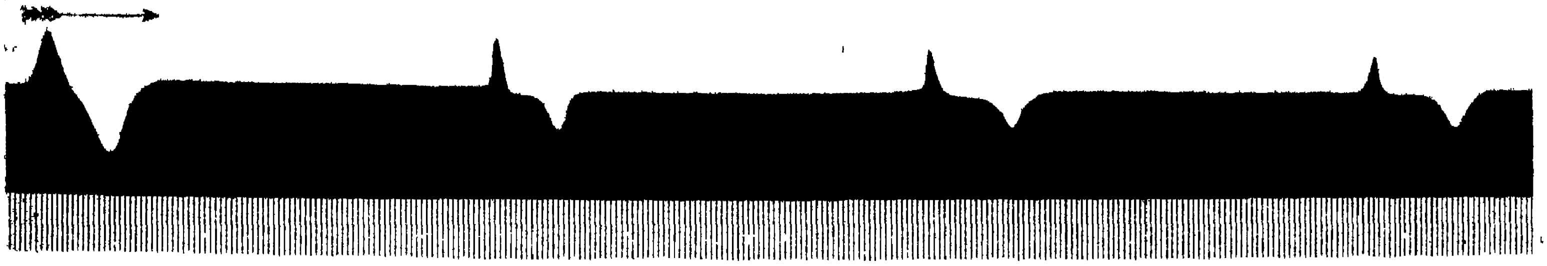


Fig 8

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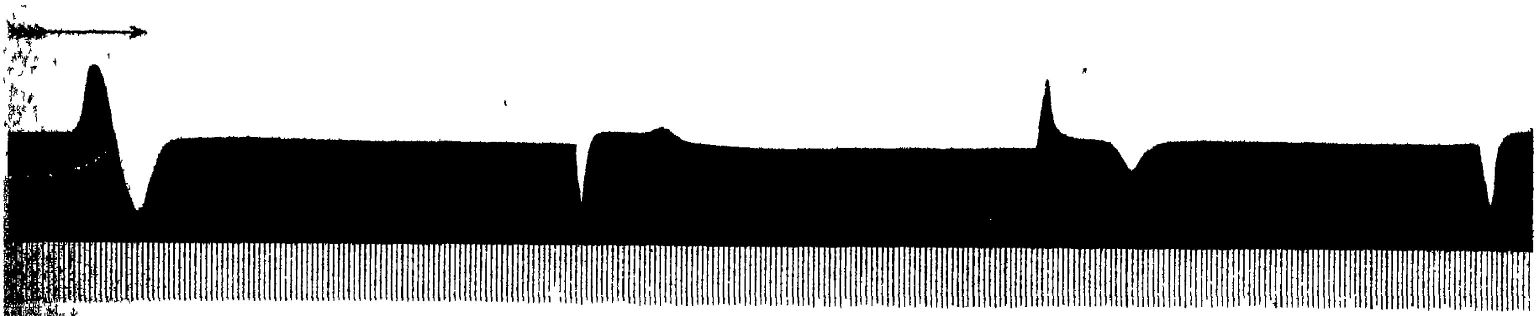


Fig 9

20 per sec

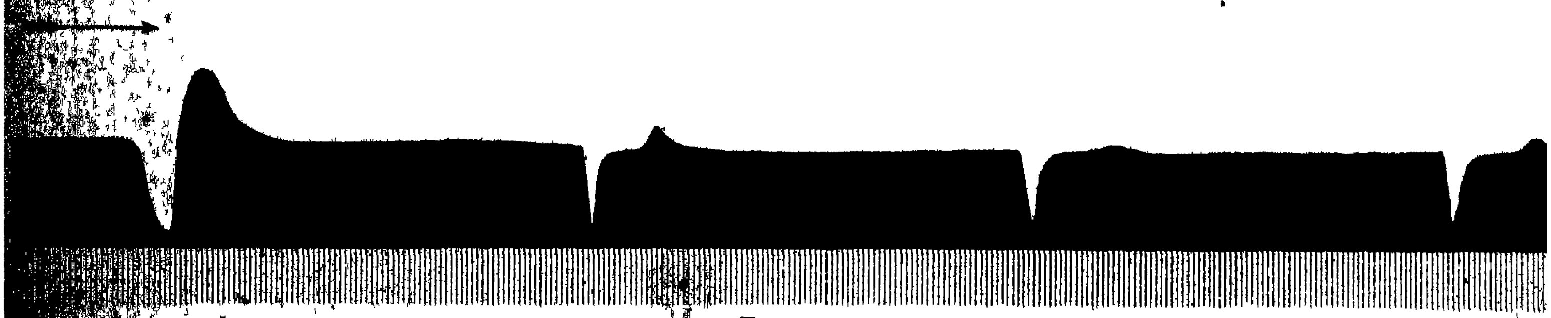


Fig 10

20 per s

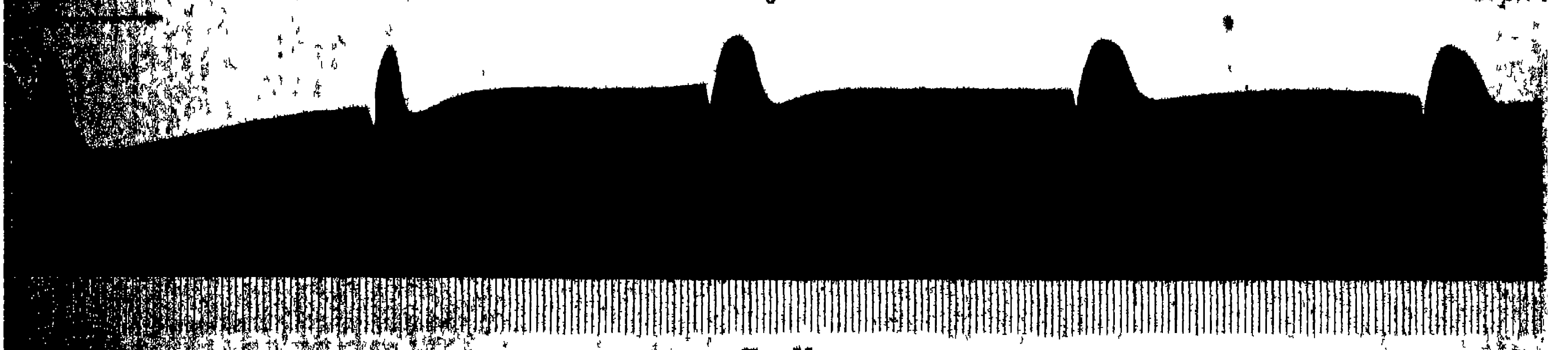


Fig 11

10 per sec

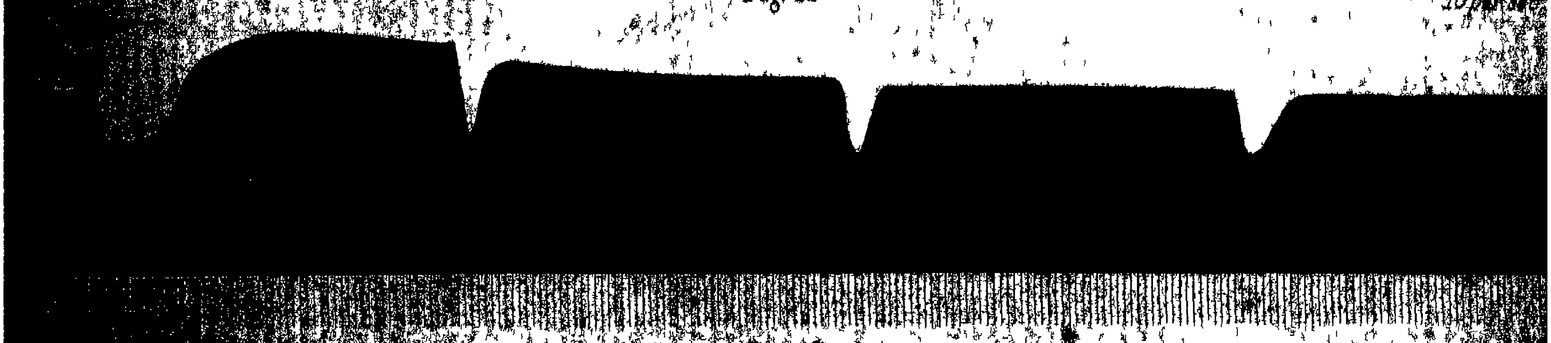
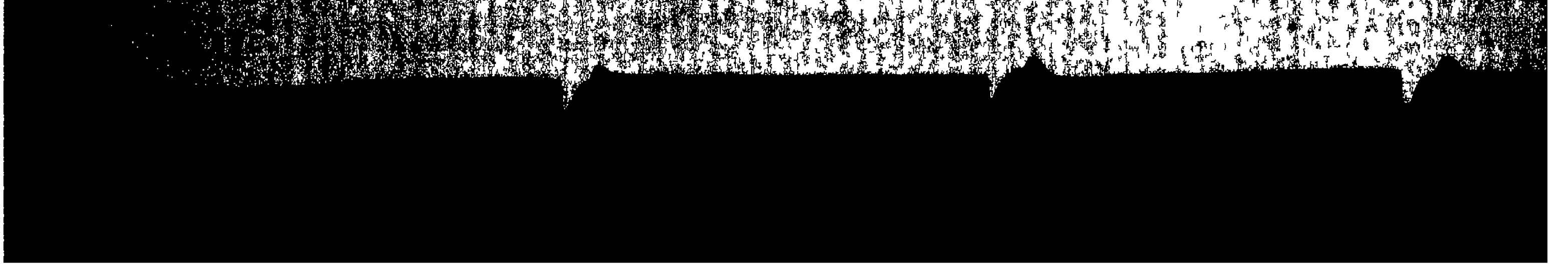


Fig 12



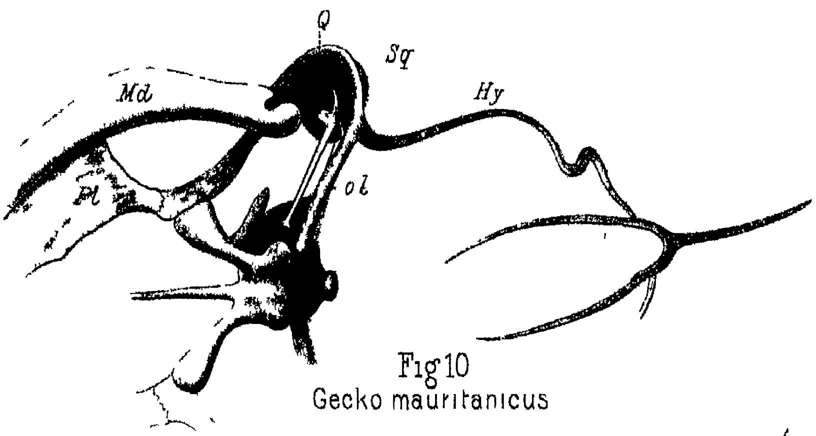
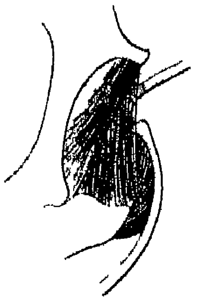


Fig 10
Gecko mauritanicus



11B
Left Right side
the same

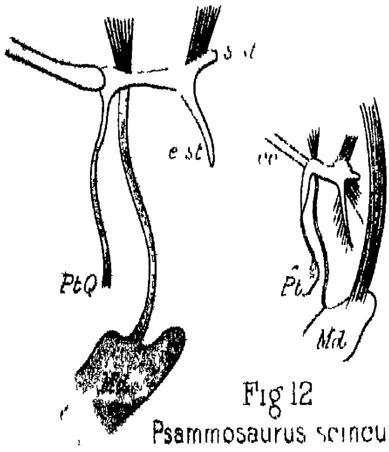


Fig 12
Psammosaurus scincus

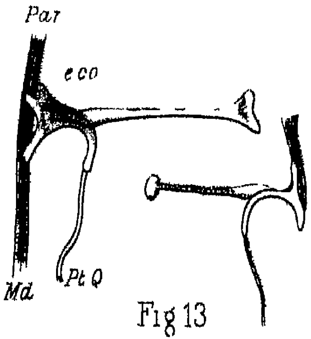


Fig 13
Teju

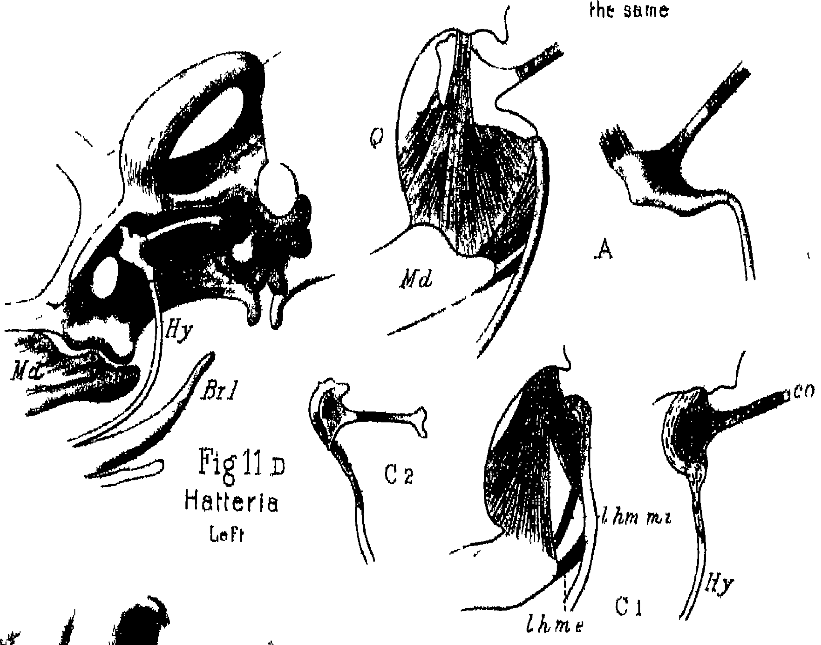


Fig 11 D
Hatteria
Left

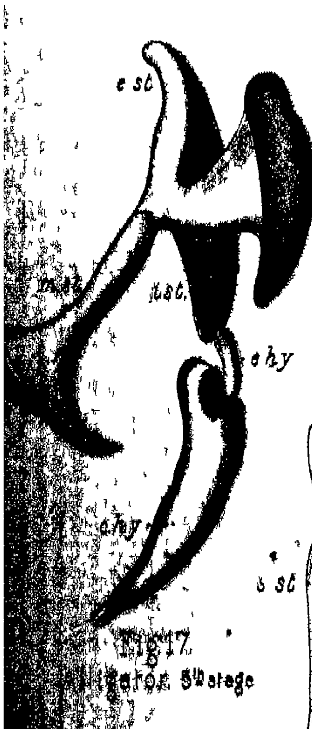


Fig 17
Alligator 5th stage

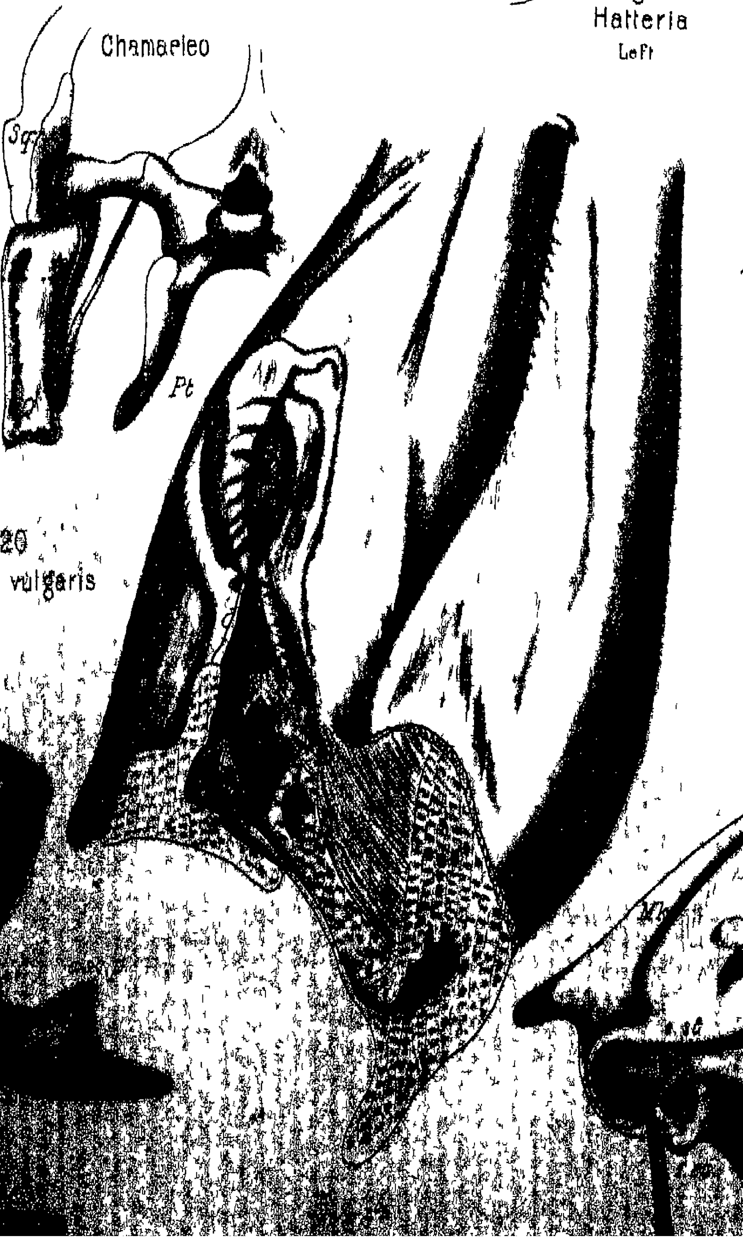


Fig 20
Chamaeleo vulgaris

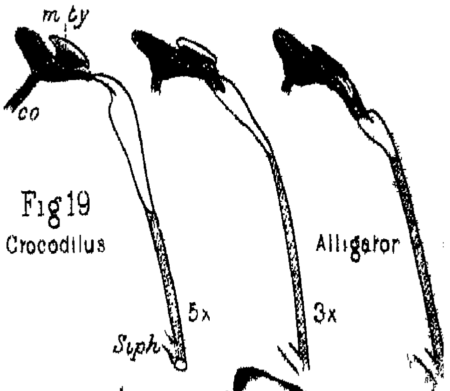


Fig 19
Crocodilus
Alligator

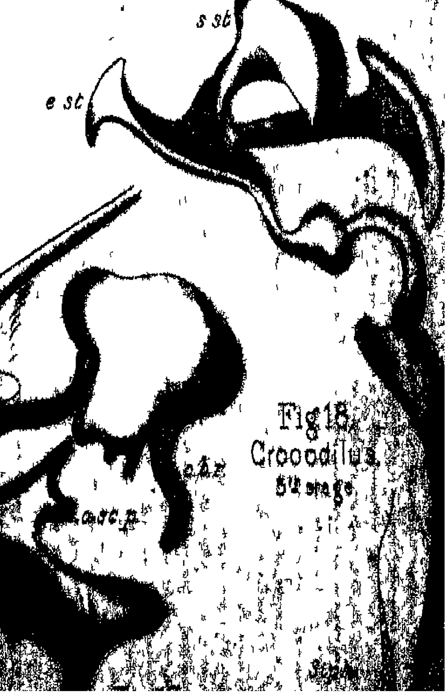


Fig 18
Crocodilus
5th stage

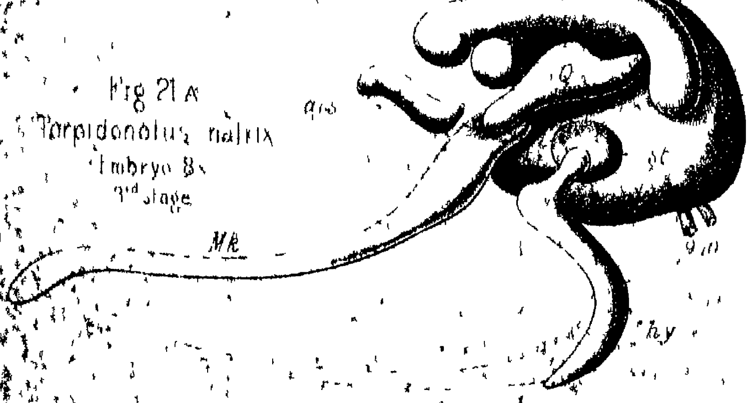


Fig 21A Torpidonotus natrix Embryo 8x 3rd stage

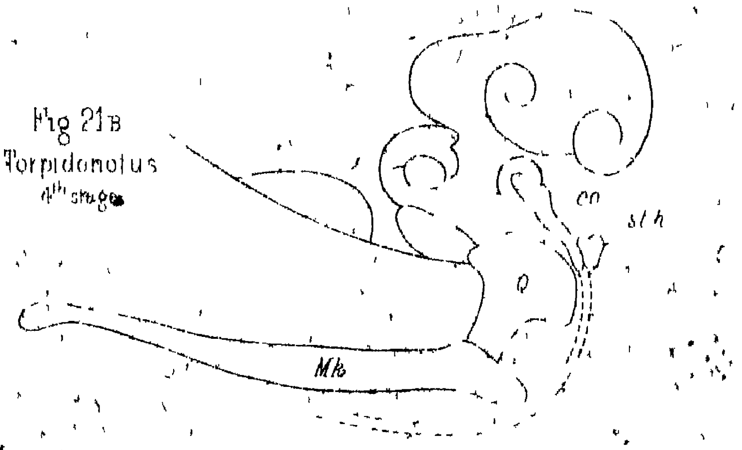


Fig 21B Torpidonotus 4th stage

Fig 27 Echidna Bruijni

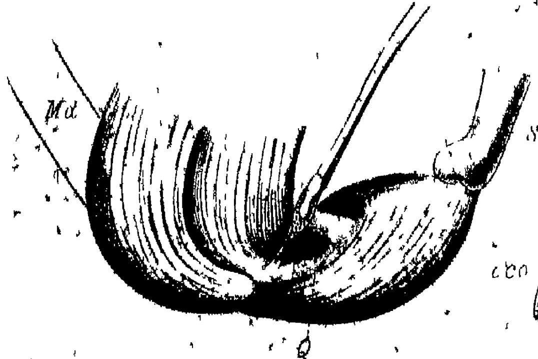


Fig 22A Pelophilus, Right inner view

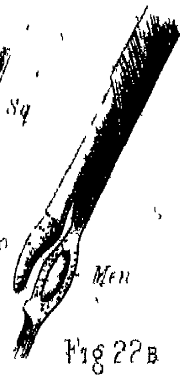


Fig 22B

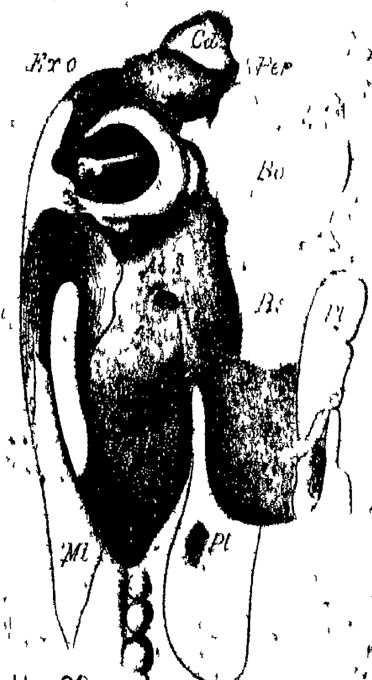


Fig 28 Orycteropus capensis Foetus,

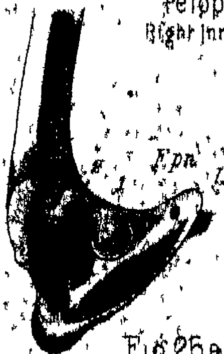


Fig 25B Regio articularis of Left Mandible Dorsal view

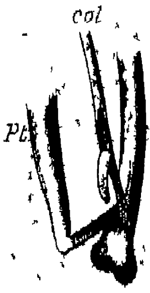


Fig 24 Crotalus Right side

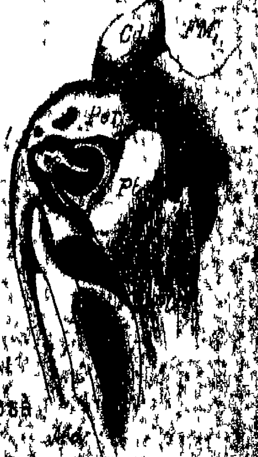
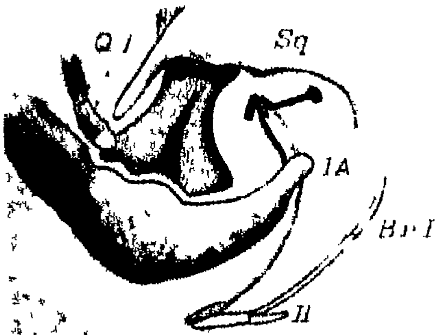
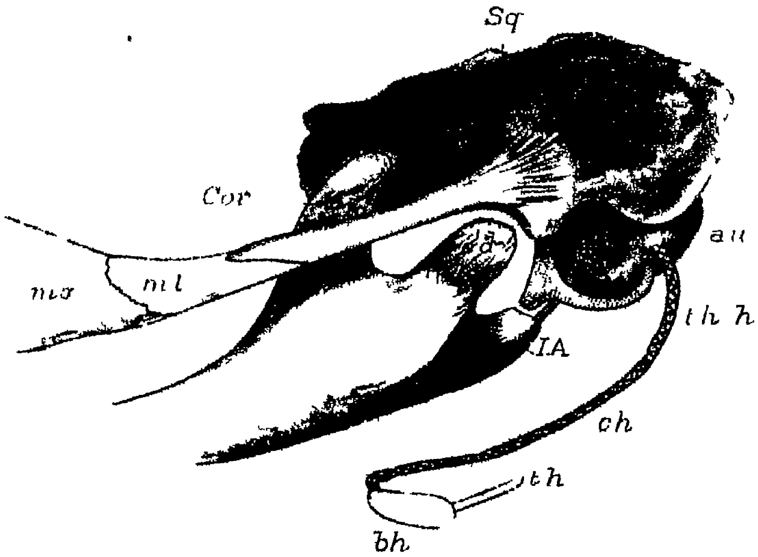


Fig 26 Echidna setosa

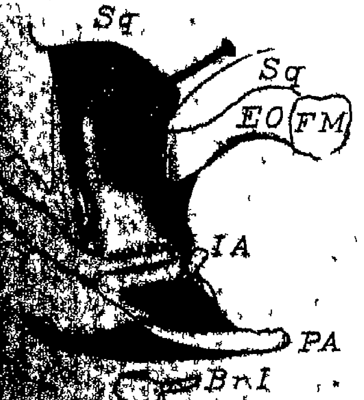
Gadow.



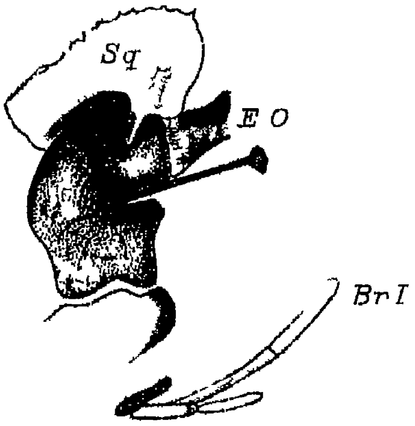
Aves



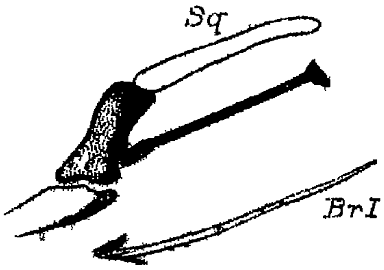
Combined diagram of Pro-Meta-and Eutheria



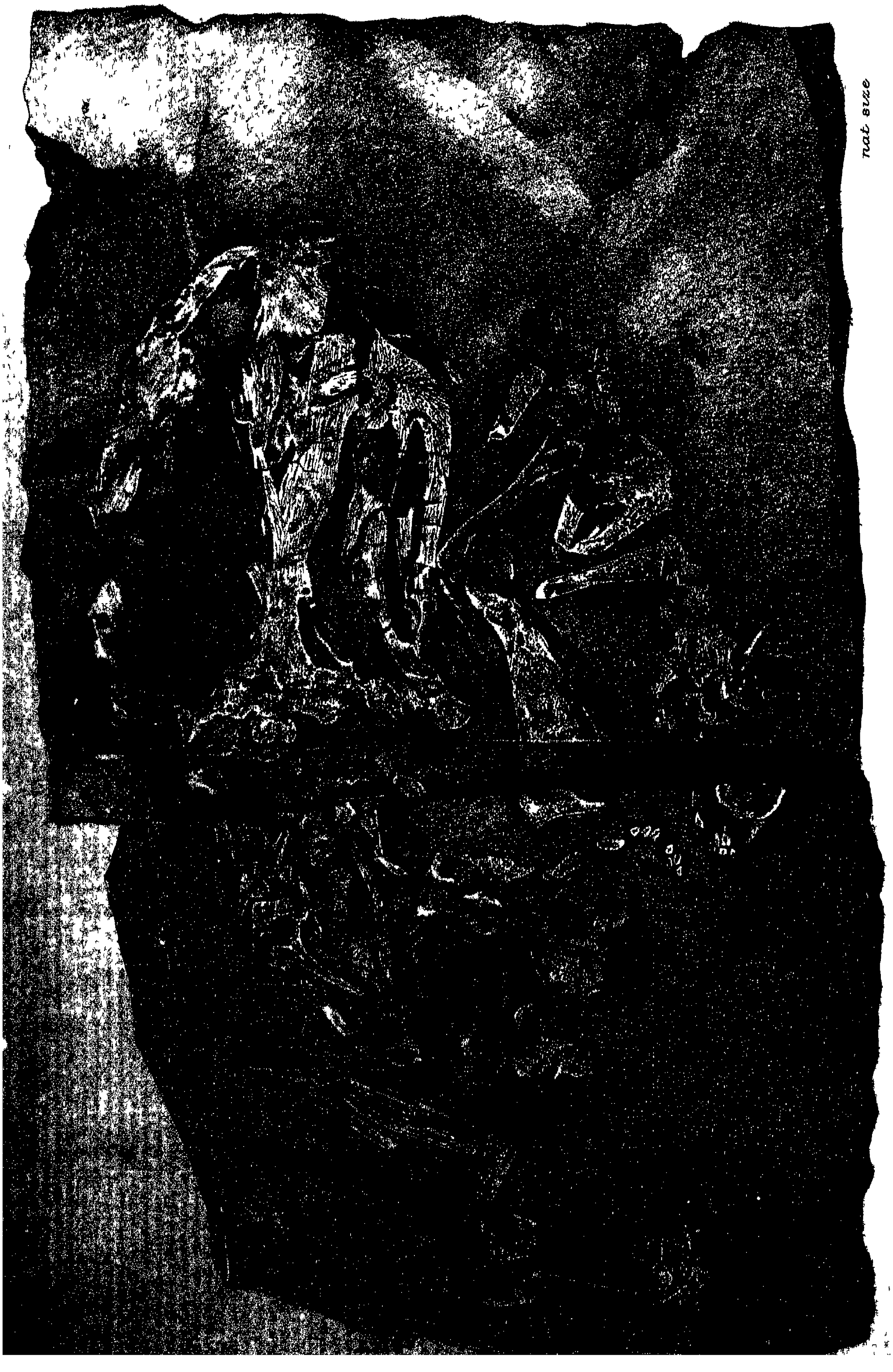
Crocodilia



Chelonia

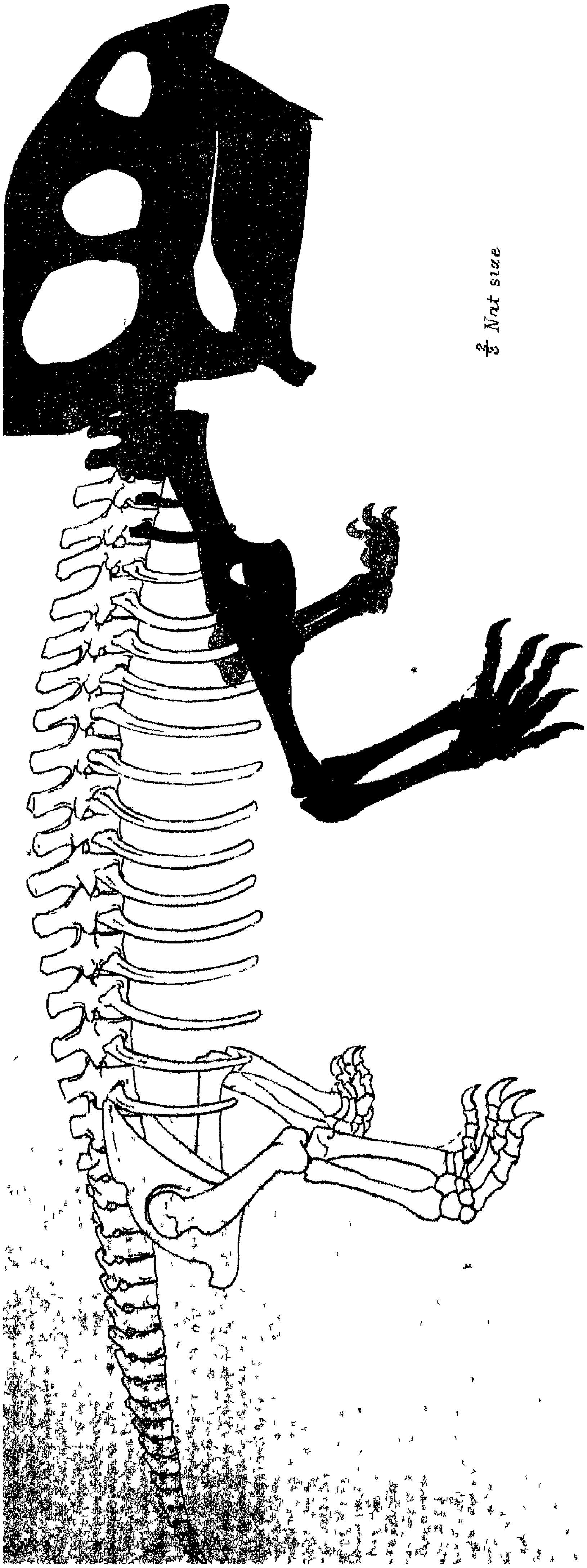


Ophidia



nat size

Skull and fore limbs of Keirognathus cordylus



$\frac{2}{3}$ *Nat size*

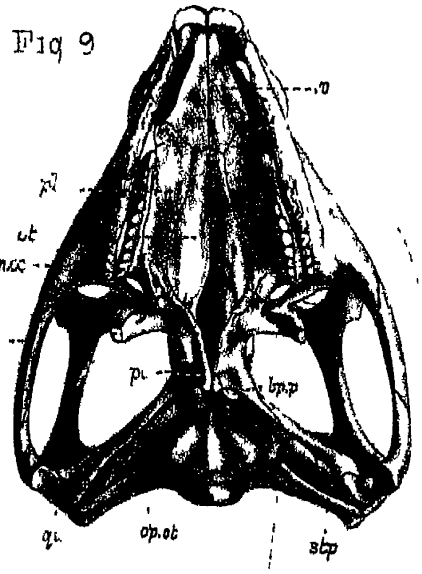


Fig 9

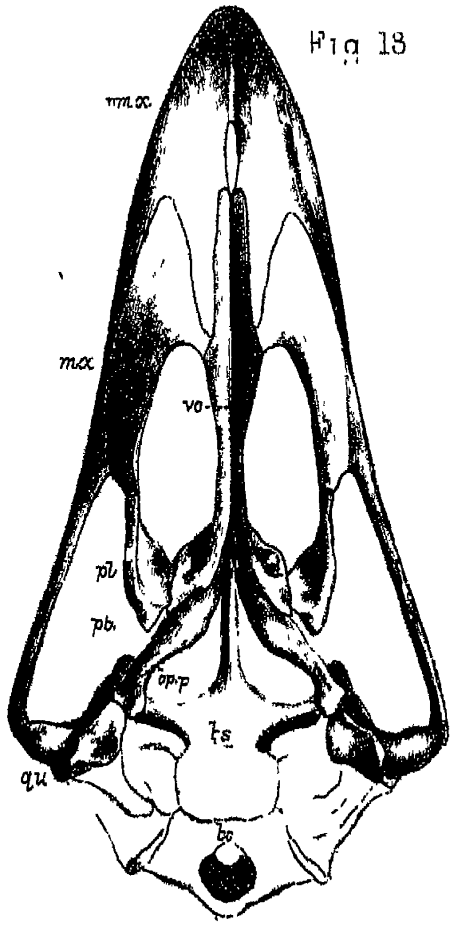


Fig 13

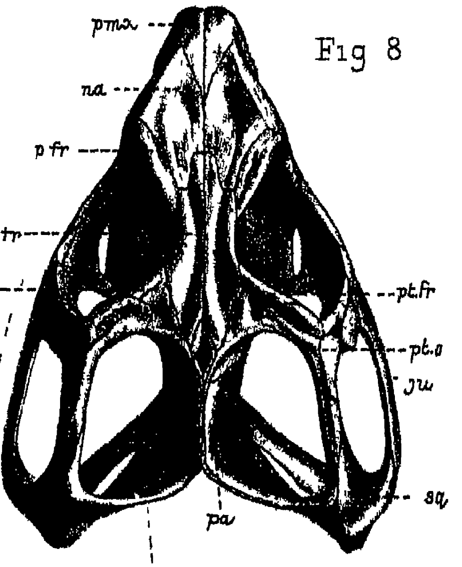


Fig 8

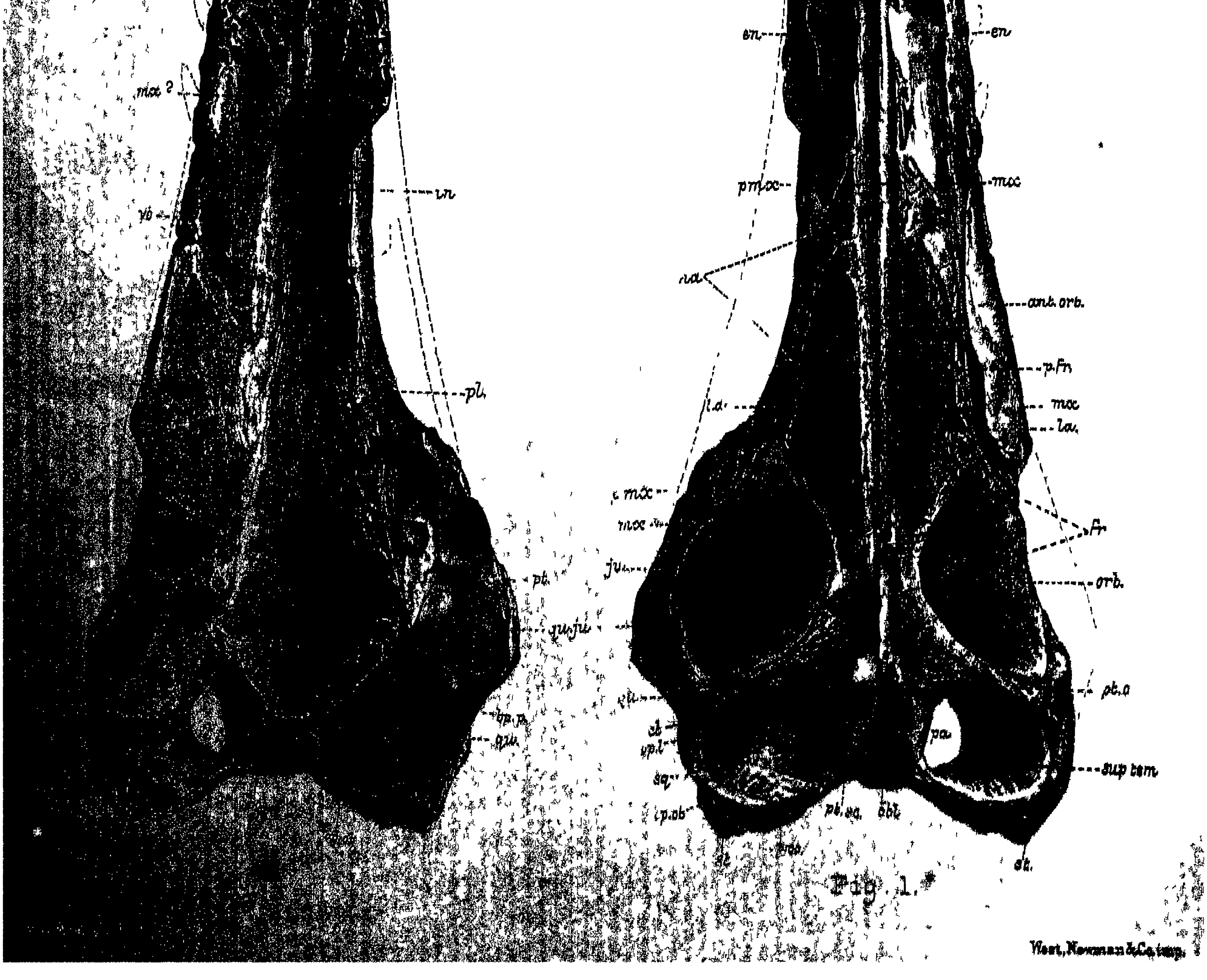


Fig. 1.

West, Newman & Co. imp.

Fig 2

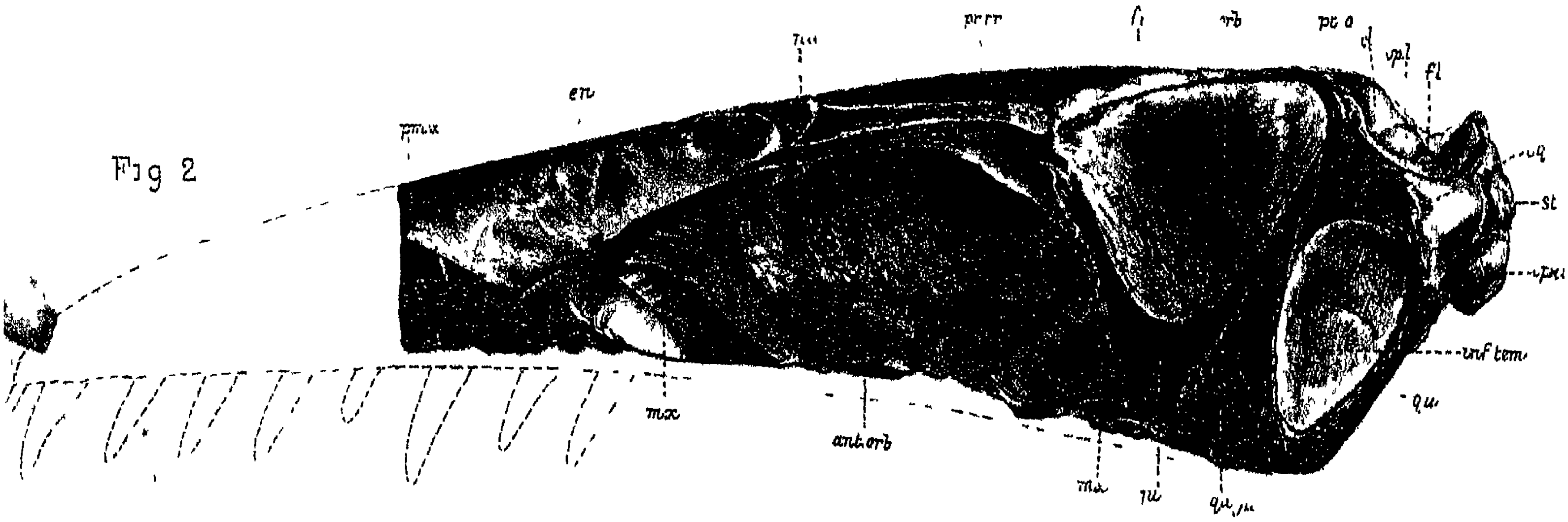
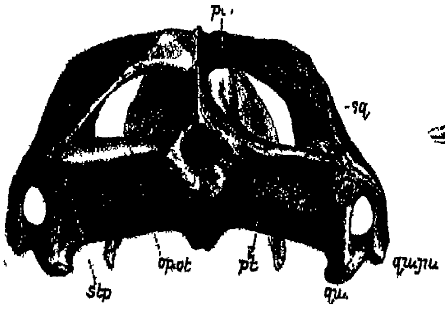


Fig 10.



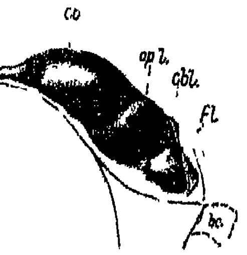


Fig 6

Fig. 11

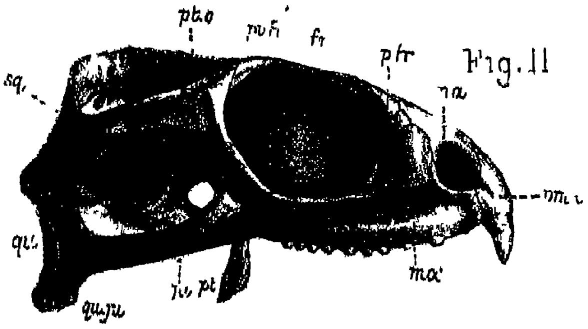


Fig 5

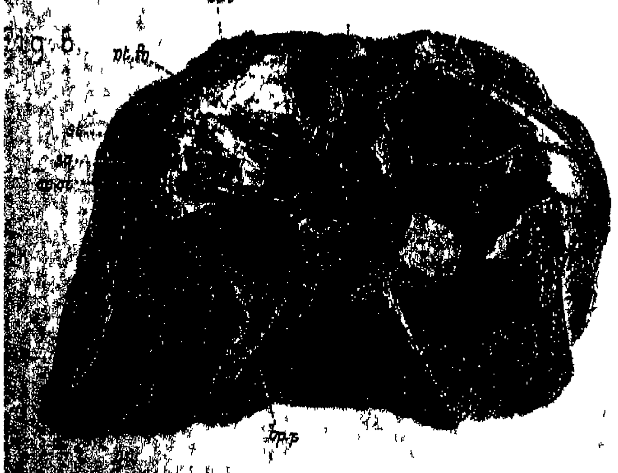


Fig 7

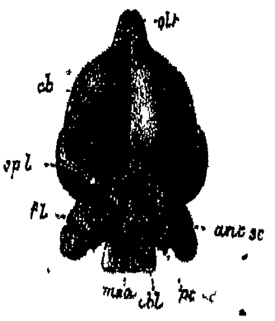
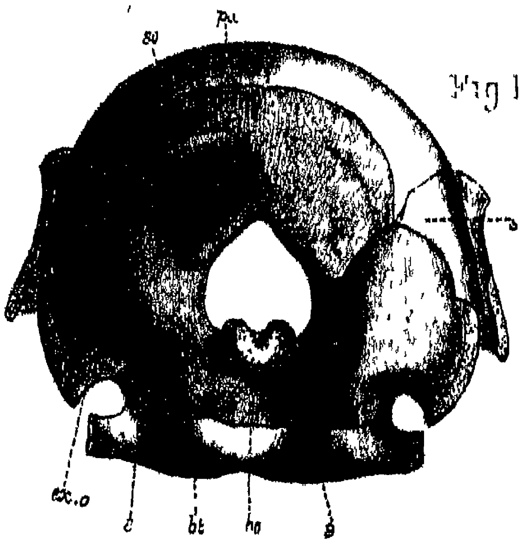


Fig 12



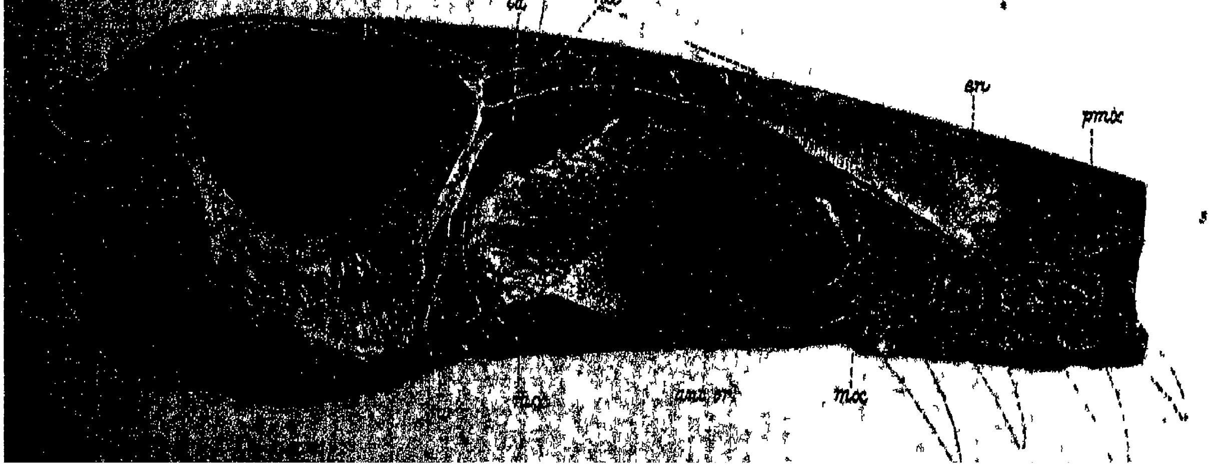
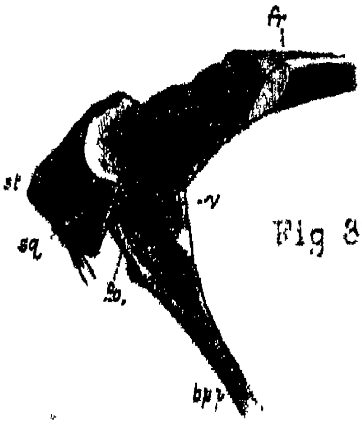
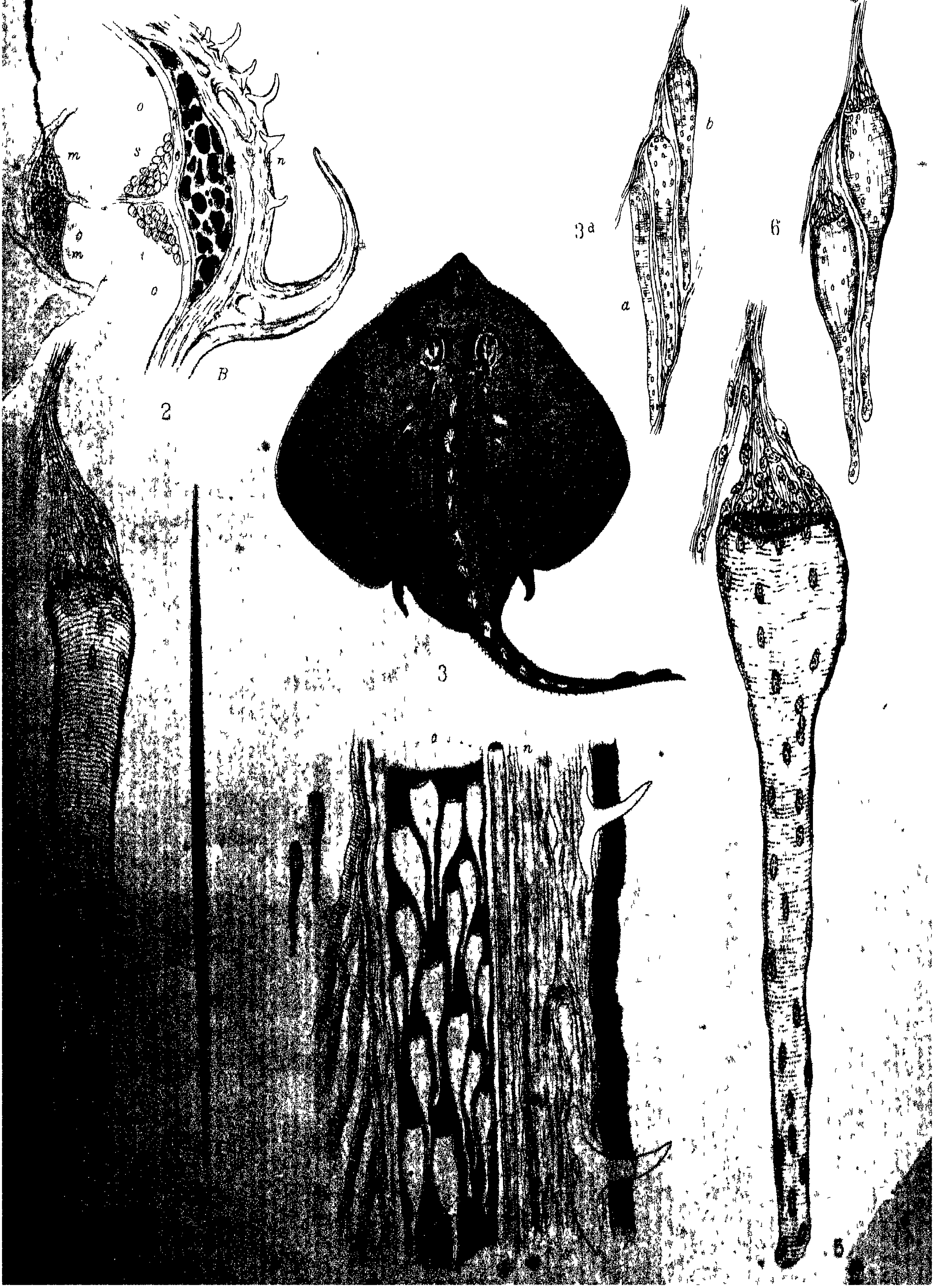


Fig 3a

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